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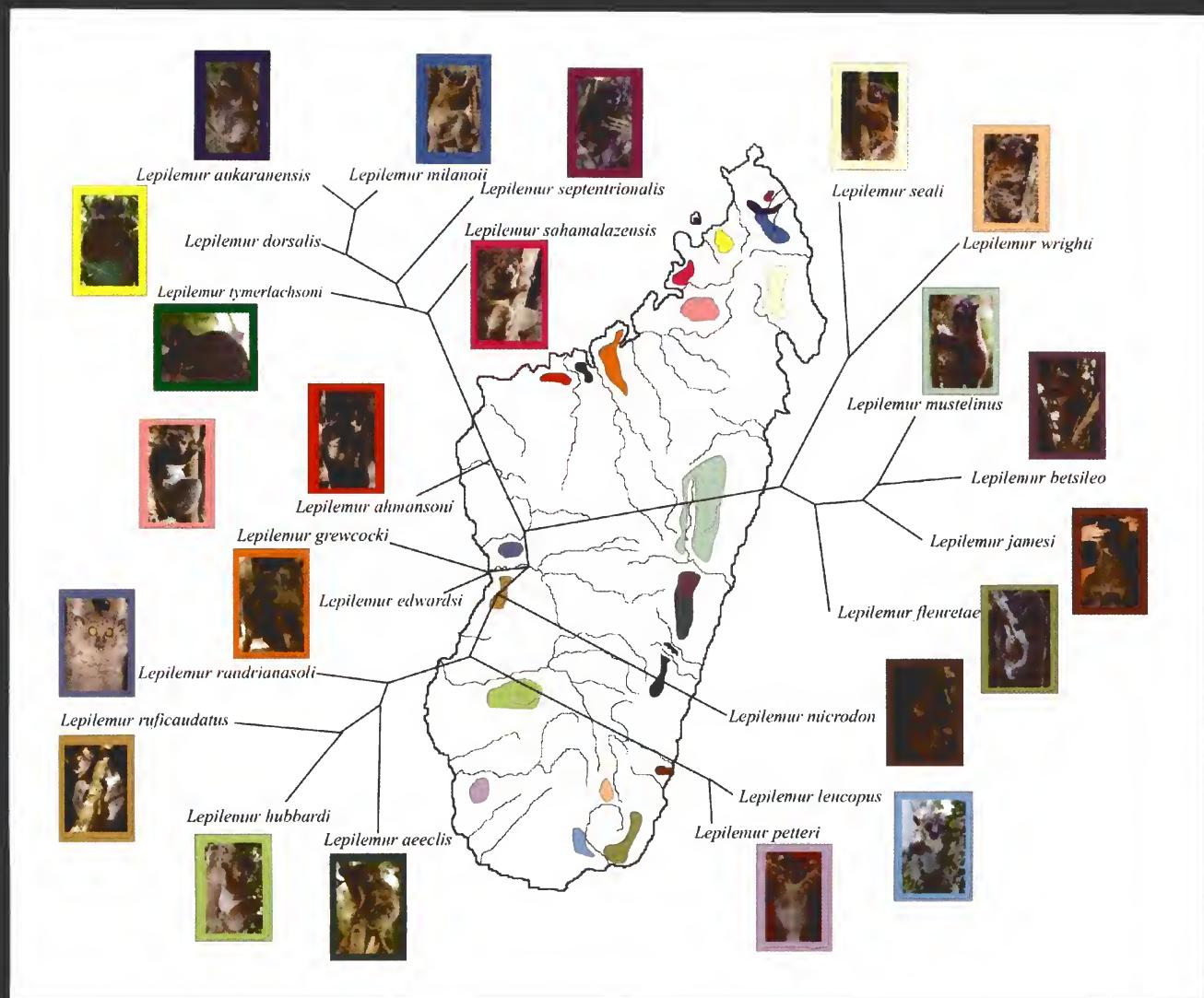
Natural Science Research Laboratory

SPECIAL PUBLICATIONS

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MOLECULAR AND MORPHOLOGICAL ANALYSES OF THE SPORTIVE LEMURS (FAMILY MEGALADAPIDAE: GENUS *LEPILEMUR*) REVEALS 11 PREVIOUSLY UNRECOGNIZED SPECIES



EDWARD E. LOUIS, JR., ET AL.

Front cover: Current distribution of the sportive lemurs of Madagascar based on molecular data. Figure prepared by Kelly Herrington, Shannon Engberg, and Runhua Lei.

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MOLECULAR AND MORPHOLOGICAL ANALYSES OF THE SPORTIVE LEMURS (FAMILY MEGALADAPIDE: GENUS *LEPILEMUR*) REVEALS 11 PREVIOUSLY UNRECOGNIZED SPECIES

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ABSTRACT

Approximately 3,800 base pairs of mitochondrial DNA sequence data (control region or D-loop, 12s ribosomal RNA subunit gene, along with a fragment including a partial segment of cytochrome oxidase subunit III gene to Leucine-tRNA gene) were used to investigate the phylogenetic relationships among the sportive lemurs (Genus *Lepilemur*) and to other lemur genera of Madagascar. The results of our analyses support a monotypic relationship of *Lepilemur* species to other lemur genera, with a sister relationship to the Family Lemuridae. Most importantly, on the basis of both molecular sequence and morphological data, our results show the existence of at least 11 previously unrecognized species of *Lepilemur*. The phylogenetic analyses presented confirm a western/eastern split among the *Lepilemur* species with the exception of the Small-toothed Sportive Lemur found at Ranomafana and Tolongoina, which is included within the western clade. These results underscore the urgency to initiate further detailed studies in previously unstudied sites throughout Madagascar in order to better define lemur species.

Key words: conservation, lemur, *Lepilemur*, phylogeography, systematics

INTRODUCTION

Due to its unique species biodiversity and to the continued pressure from human encroachment, Madagascar has been placed at the top of conservation priority lists, or hotspots (Myers 2000). Distributed throughout the island, lemurs are particularly susceptible to extinction risks due to their relatively small fragmented geographic ranges (Jernvall and Wright 1998). All lemurs are protected under the Convention of International Trade of Endangered Species (CITES) and are designated by the IUCN/SSC Red List Categories from critically endangered to threatened depending on the species (IUCN/SSC 1999). Thus, there is a pressing need to understand the taxonomy and phylogeny of lemurs so that a scientifically rational approach to their conservation and management can be developed and implemented.

The taxonomic revision of species and distributions warrants the need to consistently re-evaluate the conservation protection status of lemurs as new information becomes available (Martin 2000). Recent molecular genetic and morphological studies within the genera *Avahi*, *Cheiroleucus*, *Lepilemur*, and *Microcebus* have led to a significant increase in the number of recognized species (Andriaholinirina et al. 2006; Groves 2000; Kappeler et al. 2005; Louis et al. 2006; Rasolosarison et al. 2000; Thalmann and Geissmann 2005; Zimmermann et al. 1998). Thus, it is critical that we accurately define species and subspecies to better evaluate conservation risks and make appropriate recommendations for the management of wild populations, especially when considering the ranges of newly recognized species of lemurs. The sportive

lemurs (Genus *Lepilemur*), a group of strictly nocturnal primates that are superficially indistinguishable with varying degrees of brown, red, white, and gray pelage, are a prime example of species that until now have been largely unrecognized and underrepresented.

The only member of the monotypic Family Megaladapidae, the Genus *Lepilemur* is currently represented by 11 extant species broadly distributed across Madagascar (Appendix Ib). The taxonomy of the sportive lemurs has been revised several times (Groves 2001; Ishak et al. 1992; Jenkins 1987; Mittermeier et al. 1994; Mittermeier et al. 2006; Montagnon et al. 2001; Petter and Petter-Rousseaux 1960; Petter et al. 1977; Ravaoarimanana 2001; Ravaoarimanana et al. 2004; Rumpf et al. 2001; Rumpf and Albignac 1975; Schwarz 1931; Tattersall 1982; Thalmann 2000; Thalmann and Ganzhorn 2003), most recently by Andriaholinirina et al. (2006) who described three new species. Here, we present further taxonomic revisions by describing 11 new species. We also conducted a phylogenetic analysis of the relationships between these new species and previously recognized ones of the genus *Lepilemur*.

Although adopting a species description methodology that required a whole voucher has been the

standard, Thalmann and Geissmann (2005) presented an alternative approach through the use of only morphologic data, detailed photographs, and tissue samples. The endangered status of lemurs, all of which have been designated CITES appendix I, along with the digital and molecular technological capabilities of the twenty-first century, can eliminate the immediate requirement of whole vouchers from the wild. Nonetheless, whole vouchers can subsequently supplement the process as they become available opportunistically (e.g., raptor nests or remains of Fossa [*Cryptoprocta ferox*] predation). Due to the inability to maintain sportive lemurs as long-term live vouchers in captivity, the type series for these newly described *Lepilemur* species are represented by whole blood samples from free-ranging individuals along with a database containing all field data, accessioned sequence data, and photographs. The type series tissues and database are curated at The Museum of Texas Tech University (TK 125501-125566/TTU 104434-104499) (Appendix II).

The database referenced above, as well as additional tables and figures, also are available online at the website of Omaha's Henry Doorly Zoo. See Appendix I for a directory of the appropriate website addresses.

METHODS

Sampling.—All lemurs investigated in this study were free-ranging and were immobilized with a CO₂ projection rifle or blowgun with 10mg/kg of Telazol (Fort Dodge Laboratories, Inc., Ft. Dodge, Iowa; Figure 1; Appendix II). We recorded the location of all immobilized lemurs using a global positioning system (Appendix Ia). Four 2.0 mm biopsies and 1.0 cc per kilogram of whole blood were collected from each animal and stored in room temperature storage buffer (Longmire et al. 1992). While immobilized, a Home-Again microchip was placed subcutaneously between the scapulas of each lemur (Appendix Ia). This procedure was used to field catalog each animal with a unique recognition code in order to positively re-identify all captured individuals during any future immobilizations. In addition, morphometric measurements were taken.

We present the weight, head crown, body length, and tail length in this publication following the guidelines of Smith and Jungers (1997: Table 1). Also see Appendix Ia, the online Lepilemur Field Data Appendix, for all measurements and e-voucher photographs.

Data Collection.—Genomic DNA was extracted from samples using a phenol-chloroform extraction (Sambrook et al. 1989). From these samples, the following regions of the mitochondrial DNA (mtDNA) were amplified: the displacement loop or control region (D-loop; Baker et al. 1993; Wyner et al. 1999); the 12s subunit ribosomal RNA gene, along with a portion of the tRNA^{Pro} (12s rRNA; Hedges 1994; Wyner et al. 1999); and a fragment of the cytochrome oxidase subunit III gene (COIII); NADH-dehydroge-



Figure 1. Sample distribution map of the sportive lemurs of Madagascar.

Table 1. Morphometric data collected from sedated individuals. (Individual morphological data available online; see Appendix Ia).

Species Name	Common Name	N	Weight (kg)	Head Crown (cm)	Body Length (cm)	Tail Length (cm)
<i>Lepilemur aeeclis</i>	Aecl's Sportive Lemur	8	0.86±0.17	7.7±1.2	22.4±1.1	25.4±2.1
<i>Lepilemur ahmansonii</i>	Ahmanson's Sportive Lemur	4	0.61±0.15	6.2±1.2	20.6±1.6	23.8±0.7
<i>Lepilemur ankaranensis</i>	Ankarana Sportive Lemur	24	0.79±0.12	7.1±0.9	21.8±2.0	27.3±1.9
<i>Lepilemur betsileo</i>	Betsileo Sportive Lemur	3	1.15±0.13	7.5±0.3	25.2±0.1	27.7±1.3
<i>Lepilemur dorsalis</i>	Grey-Backed Sportive Lemur	6	0.73±0.07	7.3±0.4	22.8±1.5	27.5±0.9
<i>Lepilemur edwardsi</i>	Milne-Edwards's Sportive Lemur	11	1.10±0.11	6.7±0.6	26.3±2.7	28.5±2.1
<i>Lepilemur fleuretae</i>	Fleurete's Sportive Lemur	3	0.98±0.16	7.4±0.3	25.5±2.2	30.2±2.1
<i>Lepilemur grewcocki</i>	Grewcock's Sportive Lemur	3	0.78±0.20	6.2±0.1	24.8±2.1	28.5±1.8
<i>Lepilemur hubbardi</i>	Hubbard's Sportive Lemur	10	0.99±0.15	7.5±1.2	23.4±1.4	24.0±1.1
<i>Lepilemur jamesi</i>	James' Sportive Lemur	2	0.78±2.76	8.0±0.3	25.7±1.5	29.7±1.8
<i>Lepilemur leucopus</i>	White-Footed Sportive Lemur	18	0.54±0.09	6.5±0.7	19.6±1.4	24.2±1.2
<i>Lepilemur microdon</i>	Small-Toothed Sportive Lemur	7	1.19±0.42	10.8±2.3	27.0±2.2	26.8±3.1
<i>Lepilemur milanoii</i>	Daraina or Swimming Sportive Lemur	14	0.72±0.10	6.4±0.5	21.6±1.7	26.0±1.4
<i>Lepilemur mustelinus</i>	Weasel Sportive Lemur	27	0.99±0.21	7.9±1.4	25.8±4.0	25.2±2.1
<i>Lepilemur petteri</i>	Petter's Sportive Lemur	5	0.63±0.05	5.1±0.4	23.2±0.9	23.7±1.4
<i>Lepilemur randrianasoli</i>	Randrianasoli's Sportive Lemur	3	0.92±0.08	8.2±0.6	24.1±1.7	27.4±1.8
<i>Lepilemur ruficaudatus</i>	Red-Tailed Sportive Lemur	3	0.86±0.06	6.9±1.0	24.3±3.6	24.2±1.0
<i>Lepilemur sahamalazensis</i>	Sahamalaza's Sportive Lemur	2	0.70±0.07	6.3±0.1	19.6±0.3	23.7±2.7
<i>Lepilemur seali</i>	Seal's Sportive Lemur	6	0.95±0.08	7.4±0.9	27.3±1.4	26.3±1.4
<i>Lepilemur septentrionalis</i>	Northern Sportive Lemur	2	0.58±0.18	8.3±1.1	18.7±1.7	24.8±4.5
<i>Lepilemur tynierlachsoni</i>	Hawk's Sportive Lemur	10	0.88±0.10	6.5±0.2	23.1±1.5	24.7±2.3
<i>Lepilemur wrighti</i>	Wright's Sportive Lemur	5	0.95±0.49	8.0±1.3	25.2±3.1	25.5±1.6

nase subunits 3, 4L, and 4 (ND3, ND4L, and ND4); as well as the tRNA^{Gly}, tRNA^{Arg}, tRNA^{His}, tRNA^{Ser}, and partial tRNA^{Leu} genes (subsequently referred to as the PAST fragment; Pastorini et al. 2000). Using 50 nanograms of genomic DNA, the D-loop (555 bp), 12s rRNA (877 bp), and the PAST (2378 bp) fragments were amplified using the following conditions: 94°C for 30s; 47°C for 1 min; 72°C for 5 min for 35 cycles. Since potential nuclear insertions or mitochondrial pseudogenes within the nuclear genome can be amplified inadvertently, we chose to minimize this likelihood by amplifying both mitochondrial DNA regions as intersecting or overlapping segments (Zhang and Hewitt 1996). Consequently, the 12s rRNA fragment was generated from two amplified segments, and the PAST fragment was generated from seven amplified segments. Additionally, to further eliminate amplification of nuclear insertions, a technique that is species independent and both rapid and efficient derived from the degenerate oligonucleotide-primed PCR method (DOP-PCR; Telenius et al. 1992) was used to generate the PCR products. Adapting this LL-DOP-PCR (long

products from low quantity), the sequence data was generated for the D-loop fragments, and 12s rRNA and PAST sequence generated from overlapping segments were confirmed. The samples were electrophoresed on a 1.2% agarose gel to verify the PCR product and purified using QIAquick PCR purification kit (Qiagen; Valencia, California).

Using the BigDye terminator cycle sequencing ready reaction kit by Applied Biosystems the sequence was then run on a 7% polyacrylamide gel by an ABI 377 automated sequencer (Applied Biosystems, Inc.; Foster City, California). Four published internal sequencing primers, 12L1, 12L5, 12H2, and 12H3 (Hedges 1994), were utilized to generate the 12sRNA sequence data, and a suite of internal sequencing primers from Pastorini et al. (2000) and Pastorini et al. (2001) were used to generate the PAST fragment. Additionally, PCR and sequencing primers specific for *Lepilemur* were designed for the PAST fragment, and PCR and sequencing primers specific for lemurs were designed for the 12s rRNA and D-Loop fragments

(Appendix 1c). The sequence fragments were aligned to generate a consensus sequence using Sequencher (Gene Corp; Ann Arbor, Michigan), and the consensus sequences were aligned using ClustalX (Thompson et al. 1997). All aligned sequences are available from the first author upon request. All sequences have been deposited in GenBank and the sequence data and information are available from the referenced accession numbers (Appendix II).

Phylogenetic Analysis.—Maximum-parsimony analysis (MP) was performed for the phylogenetic study of the D-loop, 12s rRNA fragment, PAST fragment, and combined (12s rRNA and PAST fragments) sequence data with PAUP* Version 4.0b10 software (Swofford 2001). Heuristic searches were completed using the random addition sequence (1000 replicates) with the tree bisection-reconnection branch swapping routine. Gaps were considered as a fifth character in MP analyses, but were treated as missing data in the neighbor-joining analyses (NJ). Bootstrap analyses were accomplished with 1500, 1000, 2500, and 1000 pseudoreplicates with the D-loop, 12s rRNA, PAST, and combined data sets, respectively. Only nodes with greater than 50% support were reported. The maximum likelihood (ML) analyses were performed using the program DNAML in PHYLIP 3.65 package (Felsenstein 2005). Due to the large number of taxa and characters and the resulting computational intensity, we pruned the combined sequence dataset by choosing taxa from distinct clades supported in an initial NJ (Saitou and Nei 1987) analysis. The NJ analysis was performed with MEGA 3.1 (Kumar et al. 1993) using Tamura and Nei (1993) gamma distances with an α -parameter value = 0.5, which was estimated using the Yang and Kumar (1996) method; the reliability of internal branches was assessed with 1,500 bootstrap pseudoreplicates. The taxa chosen from the NJ tree for the ML analysis included 55 taxa; RANO229, a Greater Dwarf Lemur [*Cheirogaleus major*], was used as the outgroup taxon. The ML analysis of these taxa was performed using F84 gamma distances with an α -parameter value = 0.5. The reliability of the internal branches was assessed with 1,000 bootstrap pseudoreplicates.

Bayesians inference analyses were conducted using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003). The model of evolution was selected by using MrModeltest 2.2, a modified version of Modeltest 3.6 (Nylander 2004; Posada and Crandall 1998). A Markov Chain Monte Carlo (MCMC) run with four simultaneous chains and 1,000,000 generations was performed. The pattern of sequence evolution was estimated by conducting a minimum spanning network generated with the program NETWORK version 4.11 (Bandelt et al. 1999; Forster et al. 2001; Gonzales et al. 1998) and Arlequin, version 2.0 (Schneider et al. 2000). We also conducted Message Passing Clustering (MPC) (Geng et al. 2004, 2005). MPC is an agglomerative, object-oriented clustering algorithm that preserves the clustering process in a tree structure by employing the concept of message passing to describe parallel and spontaneous biological processes, such as speciation. The Kimura (1980) two-parameter nucleotide distances of the 211 *Lepilemur* samples were used as input for the MPC analysis. These distances were generated using PAUP* version 4.0b10 (Swofford 2001).

In addition to character-based phylogenetic analysis of DNA sequences, PAUP* software (Swofford 2001) was also used to calculate uncorrected pairwise distances for 12s rRNA, ND3, ND4L, ND4, PAST fragment, and 12s rRNA and PAST combined fragments ('p'). As described in Davis and Nixon (1992), Louis et al. (2006), Mayor et al. (2004), and Wyner et al. (1999), we utilized MacClade 3.01 (Maddison and Maddison 1992) and MEGA version 2.0 (Kumar et al. 1993) in a diagnostic search to designate evolutionarily significant units (ESU) using population aggregate analysis (PAA) of the D-loop (544 bp), 12s rRNA (877 bp), and PAST (2378 bp) sequence data for *Lepilemur*. With the sequential addition of each individual without an *a priori* species designation, a PAA distinguishes attributes or apomorphic characters according to the smallest definable unit (Davis and Nixon 1992; Louis et al. 2006; Mayor et al. 2004).

RESULTS

Mitochondrial DNA sequence data was completed for three fragments, D-loop, 12s rRNA, and PAST fragment (approximately 3800 bp), for 211 individuals, representing all eleven recognized species of sportive lemurs from a total of forty-one sites (Figure 1; Appendix II). All new mtDNA sequences generated for this study were deposited in GenBank and can be acquired through the accession number (Appendix II). The sequence alignments for the data sets are available from the first author upon request. The 12s rRNA fragment consists of the 3' end of the phenylalanine tRNA (22 bp) and a partial section of the 12s rRNA subunit gene (855 bp; Appendix Ig). The PAST fragment consists of the 3' end of the COIII gene (30 bp), the complete NADH-dehydrogenase subunits ND3 (348 bp), ND4L (297 bp), and ND4 (1378 bp), along with the tRNA genes, glycine (73 bp), arginine (73 bp), histidine (70 bp), serine (65 bp), and the 5' portion of leucine (47 bp; Appendix Ig). The polyadenylation of COIII and ND4 genes, insertion of base pairs between ingroup/outgroup comparisons, and other alignment characteristics between lemurs and *Homo* are consistent with Pastorini et al. (2000).

Based on the phylogenetic inferences of the NJ, MP, and ML analyses of four sequence alignments (D-loop, 12s rRNA, PAST, and 12sRNA-PAST fragment combined), three major *Lepilemur* subgroups are represented, differentiating the eleven recognized sportive lemur species (Figures 2-4, 6-7; additional figures are available at <http://www.omahazoo.com>). The first subgroup corresponds to the eastern sportive lemurs, *L. mustelinus* and *L. microdon* (the distribution of *L. mustelinus* and *L. microdon* is based on Andriaholinirina et al. (2006) and Mittermeier et al. (2006); Appendix Ib). The second subgroup includes the western and southern sportive lemurs, *L. edwardsi*, *L. aeclis*, *L. randrianasoli*, *L. ruficaudatus*, and *L. leucopus*, respectively. The remaining subgroup consists of the recognized northern sportive lemurs, *L. septentrionalis*, *L. ankaranaensis*, *L. dorsalis*, and *L. sahamalazensis*. There is high bootstrap support for the MP and NJ analysis with respect to the topology of the genera and

species (Figure 2). In order to verify that our samples are indicative of the three newly described species in Andriaholinirina et al. (2006), we used GenBank to BLAST cytochrome B subunit gene sequence generated for our data set. This confirmed that our samples are representative of those species (GenBank Accession DQ529452-DQ529459; Andriaholinirina et al. 2006). Additionally, 11 distinct subpopulations were identified within the currently recognized *Lepilemur* species distribution. Each subpopulation is geographically defined by rivers which isolate them by acting as barriers to the recognized species. The results from the population aggregate analysis of the D-loop, 12s rRNA, and PAST sequence data are presented in Tables 2A-C and 3A-C, respectively (the complete diagnosis from the PAA for the D-loop, 12s rRNA, and PAST sequence data are available online; see Appendix Ie). Multiple diagnostic characters define each *Lepilemur* species, along with the 11 newly described species (Tables 2 and 3). A review of the morphometric data for the 22 species of sportive lemurs is presented in Table 1 (detailed morphological measurements of the individual animals are available online; see Appendix Ia). The complete uncorrected 'p' distance and the Kimura two-parameter distance measures are presented in Appendix Id.

The MP, Bayesian, and MPC analyses are presented in Figures 2 and 3 (also see Appendices Ia and Ii). All analyses differentiate 22 *Lepilemur* species, including 11 new species. The minimum spanning network presents diagrammatically the speciation among the 22 sportive lemurs (Figure 5). The ML tree was estimated from the combined 12s rRNA/PAST alignment from a subset representing the haplotypes within the data set, and corresponds to the other phylogenetic inferred trees (Figure 7). There is high bootstrap support for the ML analysis with respect to the topology of the genera and species. Specific resolution of sportive lemurs based on phylogenetic inference parallels geographic separation into western, eastern, and northern groups with the exception of *L. microdon* which is aligned with the western group.

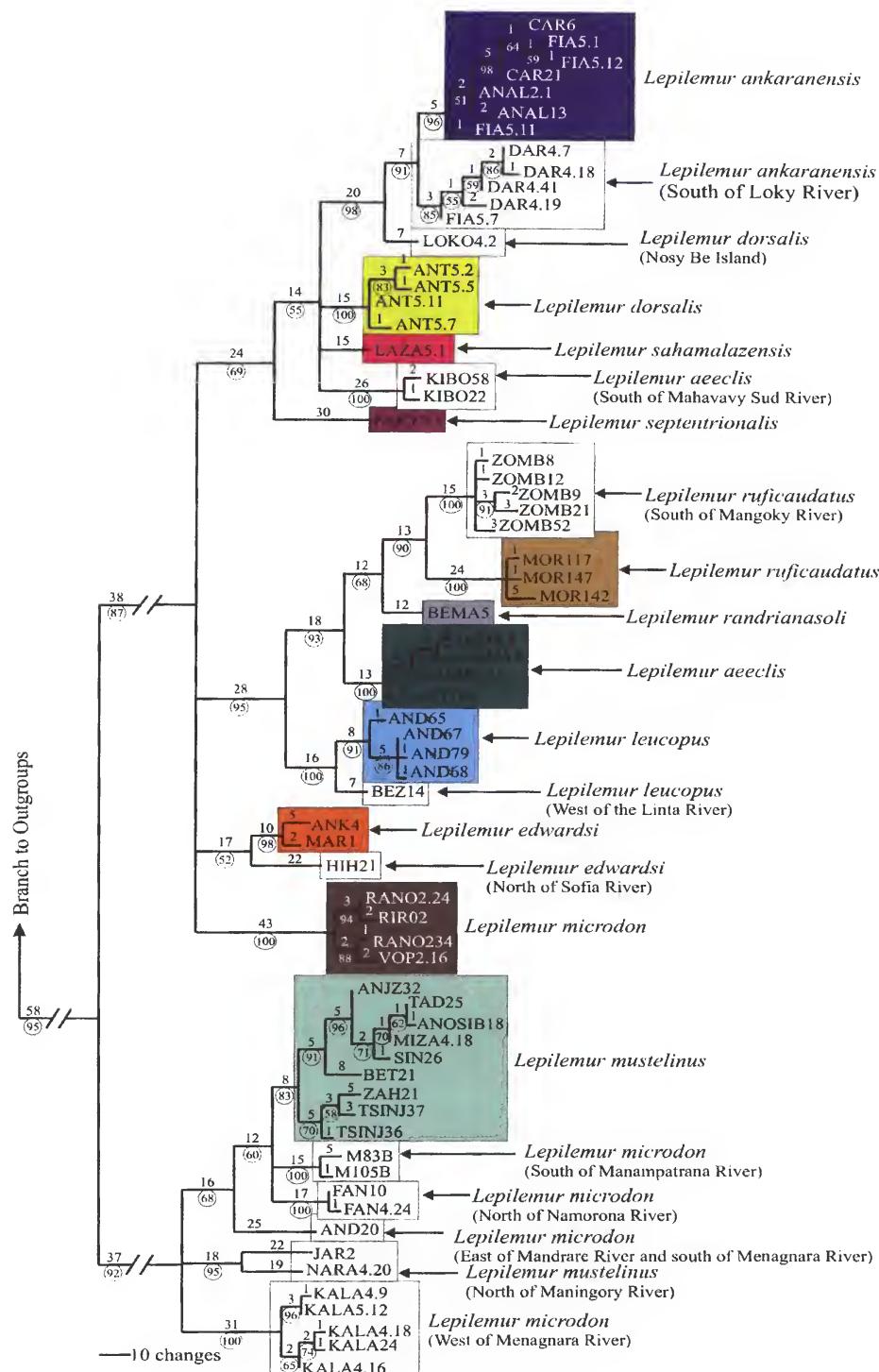


Figure 2. Neighbor-joining phylogram derived from D-loop DNA sequence data from 67 haplotypes from the 211 *Lepilemur* individuals. Species designated according to the distribution in the current literature (Andriaholinirina et al. 2006; Mittermeier et al. 2006; Appendix 1b). Values above branches indicate number of changes between nodes. Values below branches indicate support of bootstrap pseudoreplicates. Length = 1,698; CI = 0.4346; RI = 0.8299; RC = 0.3607; HI = 0.5811.

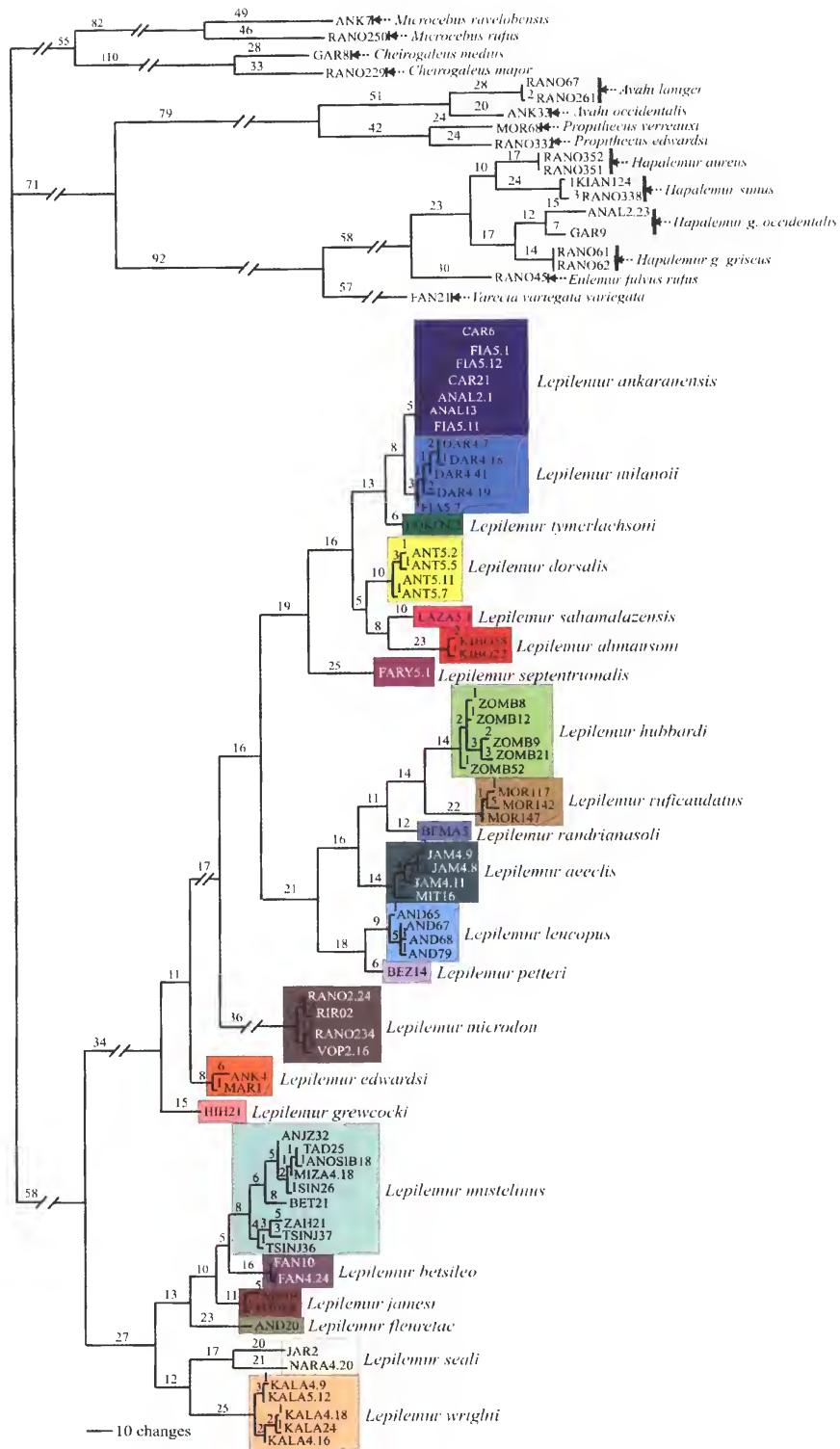


Figure 3. Phylogeny derived from D-loop fragment sequence data from 67 *Lepilemur* haplotypes (one of 80 most parsimonious trees). Values above branches indicate number of changes between nodes.

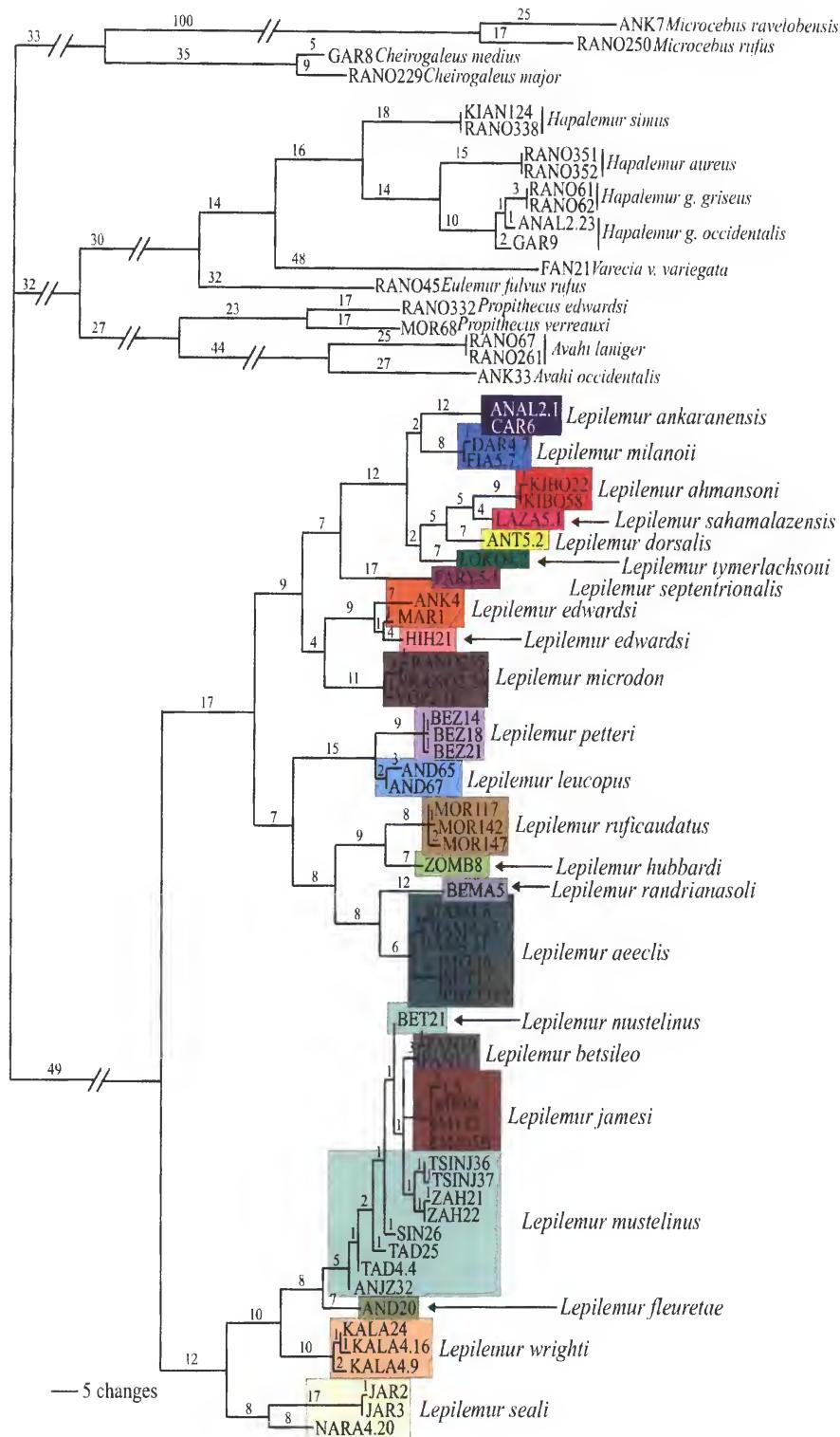


Figure 4. Phylogeny derived from combined 12s rRNA fragment sequence data from 54 haplotypes from 211 *Lepilemur* individuals (one of 128 most parsimonious trees). Values above branches indicate number of changes between nodes. Length = 1,080; Cl = 0.5139; RI = 0.8629; RC = 0.4434; HI = 0.5132.

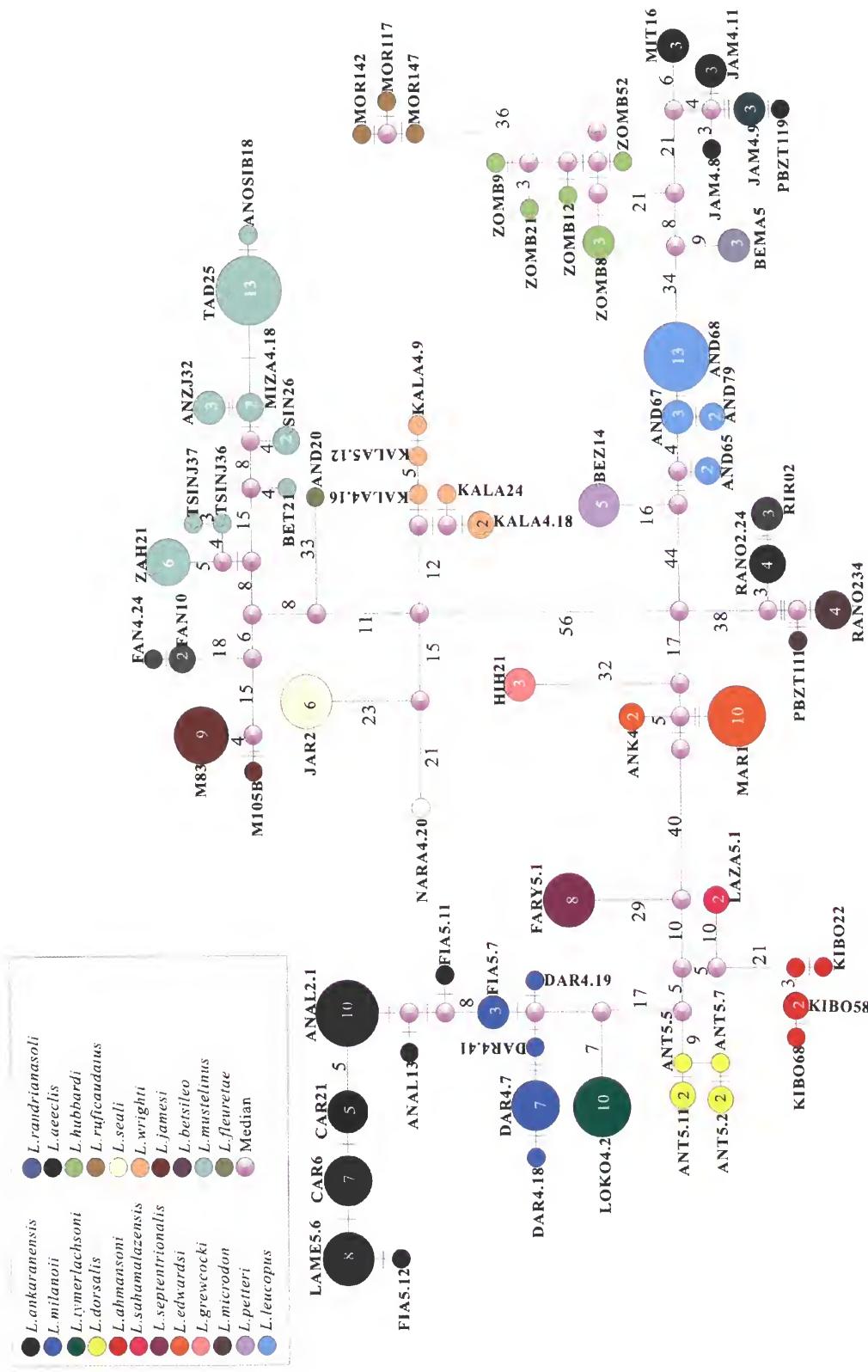


Figure 5. Minimum spanning network of *Epilemur* haplotypes calculated using Arlequin Version 4.11 and Network Version 2 and Network Version 4.11. Identification numbers denote haplotypes corresponding to Appendix II. The minimum number of mutational steps separating matriarchal lines is indicated. Nucleotide substitutions are indicated by dashes. The number of nucleotide differences in their connecting lines (more than 10) is indicated when they are more than one. Missing intermediates are indicated by gray circles. The size of circles approximates the number of individuals with matching haplotypes (circles without any number represent one individual).

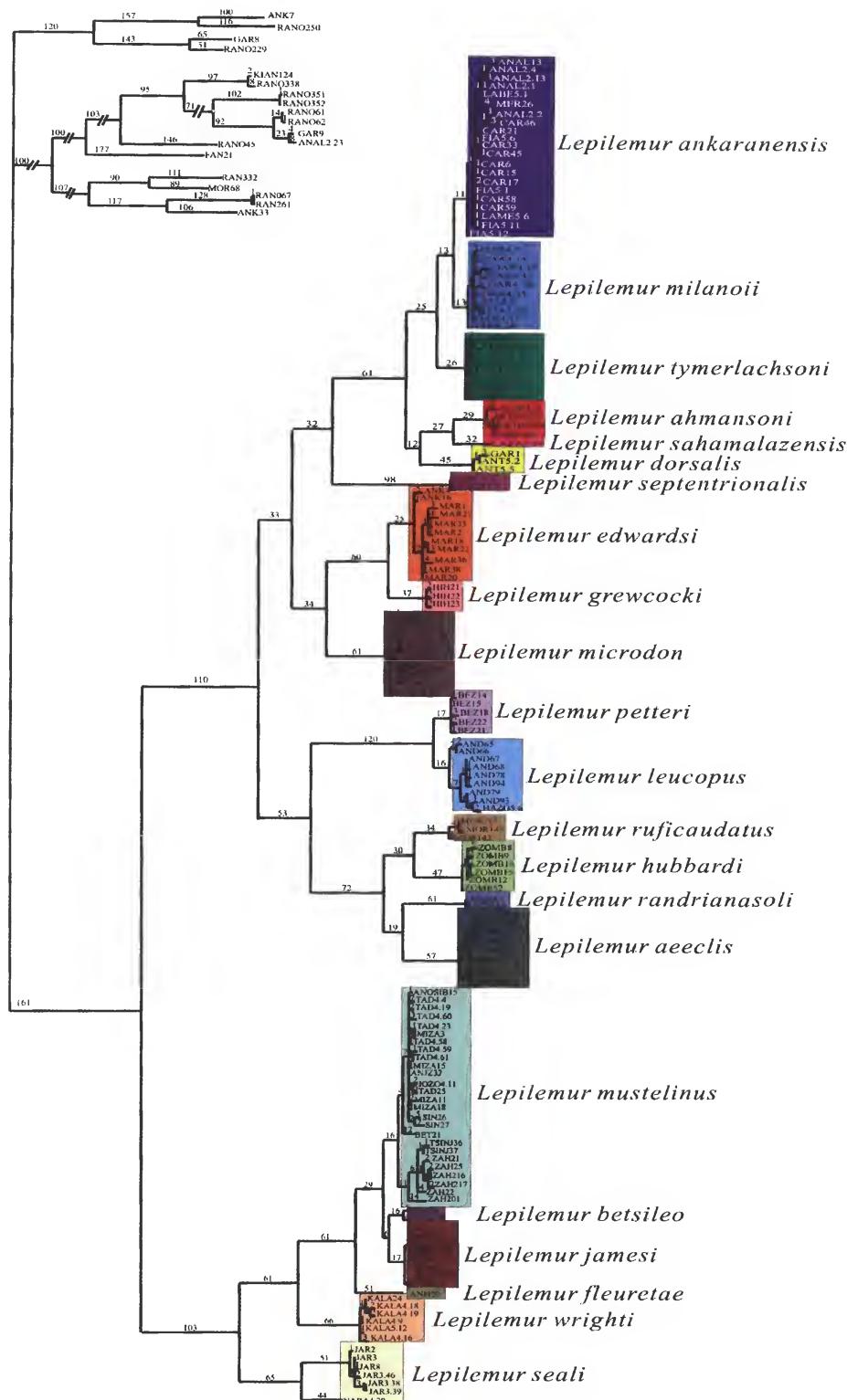


Figure 6. Neighbor-joining phylogram derived from PAST fragment sequence data from 211 *Lepilemur* individuals, representing 156 haplotypes (the phylogram presented maintains branch lengths proportional to the number of changes).

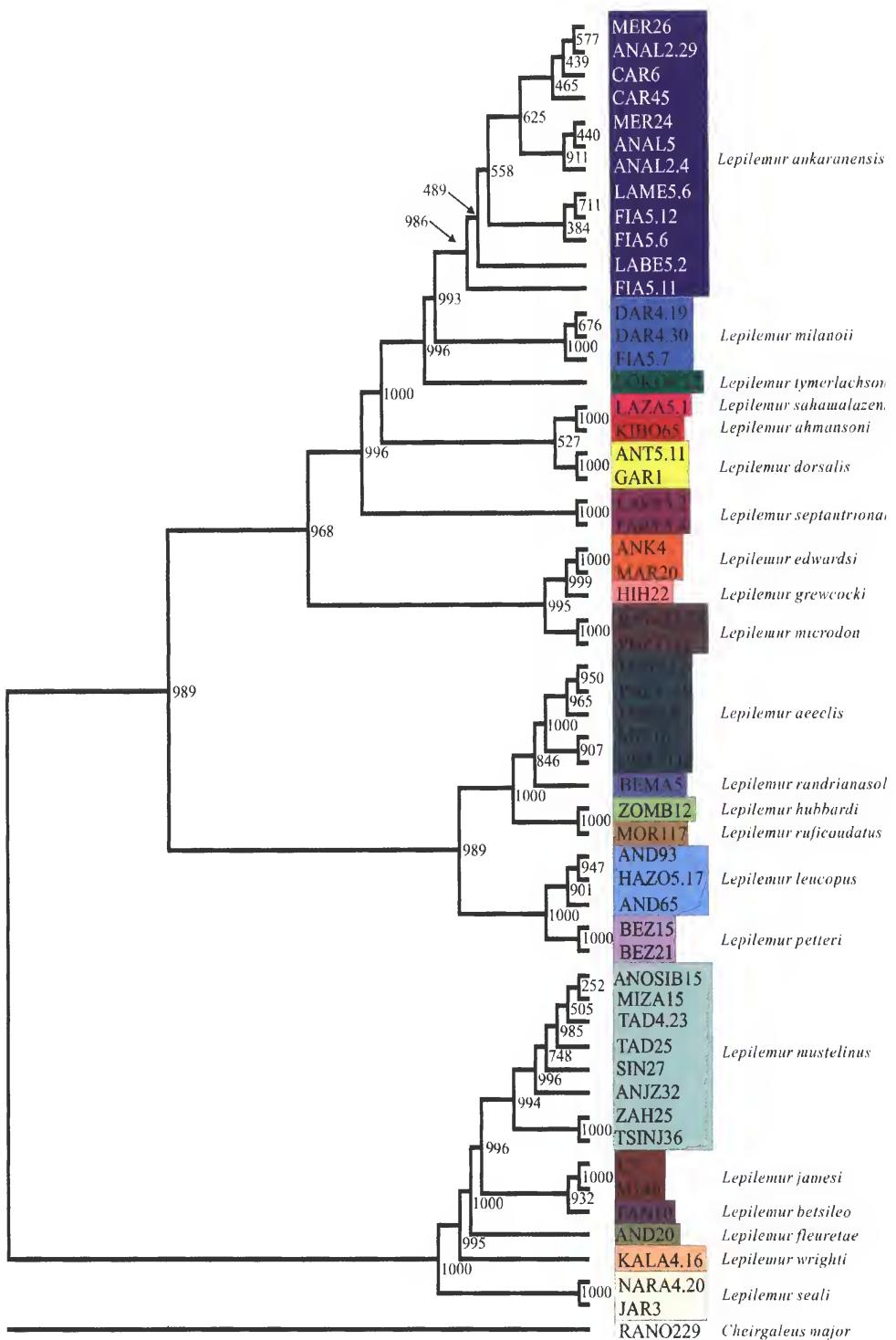


Figure 7. Maximum-likelihood phylogram derived from combined 12s rRNA and PAST fragment sequence data from 55 *Lepilemur* individuals. The phylogram is rooted on the left and branches to the right. Bootstrap support values are indicated at the nodes. Lepilemur species are color-coded: *L. ankaranensis* (purple), *L. milanoii* (blue), *L. tmymerlachsoni* (green), *L. sahawalzeni* (red), *L. ahmansi* (orange), *L. dorsalis* (dark purple), *L. septentrionalis* (light purple), *L. edwardsi* (dark red), *L. grewcocki* (dark blue), *L. microdon* (dark grey), *L. aeeclis* (black), *L. randrianasol* (dark blue), *L. hubbardi* (green), *L. ruficaudatus* (brown), *L. leucopus* (dark blue), *L. petteri* (dark red), *L. mustelinus* (dark blue), *L. jamesi* (dark red), *L. betsileo* (dark blue), *L. fleuretae* (dark red), *L. wrighti* (orange), *L. sealii* (dark blue), and *Cheirogaleus major* (grey).

Table 2A. Diagnostic nucleotide sites from the D-loop Pairwise Aggregate Analysis (PAA) of Lepilemur.

	111111111111111111112222222222233333333445555
	1112233333444455559000111122222233339911445677888900011588979335
	1089152347834670457893470347901345691456838280718014569018255784413452
ANAL2.1	CTCAACGCTATTAAA----AACCTTCCTGGAGC-ACCCAAATTGCAACATTAAATCACCTCAAAACP
DAR4.7T.....----T.....-G.....
LOKO4.2T.....----T.....-.....-.....T.....-.....
FRAY5.01T....C.G.C-CC--T..--A....---.....G....C.....A.....
ANT5.2TA.....----T.....A...T-.....C....T...A.....GA.
LAZA5.1TA.C.....C-T--.....AAG..-.....C..T.....T...A.....T..
BEZ14A.....C-T.....A...T-T.....TTT....C....T...A.....
AND65	...G.....C-T.....AA..T-T.....TT.....T...G.....
MOR117-C.....C-C--G.....A...GGC...GG...TCC.....GCTA..A.....GC..
ZOMB8-.....C-C--.....A...-C...GG...GTTG..C..GTC...G.....T..
BEMA5AT..A---C-C--G.....T..AA..CC..GG...CT..A.C....C...C.....
MAR1A...CAT..C-C--....C..CA..AGC-...CCC.....T...A.....
HIH21A...CAT..C-C--....C..A..AGC-...CTG.....C...T...T.....
KIB022TA.....C-T--.....AAGA..-.....C.....C....T...A.....
JAM4.27	...G.A.C.....C-C--....C..A...-T...GG...T...AC..G.T...A.....
TAD25TAAC.CA.C.AACCA..T.....AAC.GG...CA.TCT...A..C...ATCAC..T..
M83BTAAC.CA.C.AACCA..T.....C..AAC.GA...CA.TCT..CCG...C...A..AC..T..
FAN10T.AC.CA.C.AACCA..T.....C..AAC.GA..GCA.TCT..CCG...C...A..AC..T..
AND20	.C....AACCCA.CGAACCA.....C..AGC.GG...C-..T...ACG.C..AGA..AC..T..
RAN0234AA.G.CAC..C-CTG...TG.T...-----C.....T...A..T....A
KALA24TAA..CA.C.TCACCG.T..C..C..TAA..GGT...A.TT....C..TC..T.G..ATC.C..
JAR2	T..T...TAC.CA.C.AGCCT..A..C..C..T.GT.GGT..CAAAC...A...-....A..AC..T..

Table 2B. Diagnostic nucleotide sites from the 12s rRNA Pairwise Aggregate Analysis (PAA) of Lepilemur.

	1112222233333334444445556666777777778
	156614534479134468991133689035746892455666895
	6830608450204040999143823988066916433607168664
ANAL5	AAGACTCTAACAGAATCCCGTAAATATAACAAACACCCGGT
DAR4.7G..T.....T...
LOK04.2A.....T....I.....C
FARY5.1	.G.G.G.C.....G.....C.C....T.....
ANT5.2T.....T...A.
LAZA5.1C.....T.....T.....T.....
BEZ14G.....T.....C.G.....
AND65T.....C.G.....T...
MOR117T.G.....
ZOMB8G.....C.C.....
BEMA5	T.....T.....A.T..G.C.G.....C.....
MARIC.....T.....
HIE21C.....T.....
KIB022C.....T.T...G.T...G...
JAM4.27T.....C.G...C.....
TAD25	C....C.....C.G..T.....C.T..A...
M83B	C...TC.....C.A...T.....C.T..A...
FAN10	C....C.....CC.A...T.....C.T..A...
AND20	C.A..C.....T.....C.A.C.T.....C.C..A...
RAN0234T.G..G.....C.....T.....G..A..
KALA24	C....C.....A.....C.A..T.....T.T..A...
JAR2	GT...C.....A.....CGA..GTG..C..C....A..

Table 2C. Diagnostic nucleotide sites from the PAST pairwise Aggregate Analysis (PAA) of Lepilemur.

Table 2C (cont.)

Table 3A. Summary of Population Aggregate Analysis (PAA) D-Loop diagnostic sites for *Lepilemur* species. Refer to Table 2A. *No Character or Attribute is available for this fragment.

Species	Fragment Size (bp)	PAA base pair location
<i>Lepilemur ankaranensis</i>	540	*
<i>Lepilemur milanoi</i>	540	129
<i>Lepilemur tynierlachsoni</i>	538	117, 301
<i>Lepilemur septentrionalis</i>	536	43, 46, 99, 113, 114, 247
<i>Lepilemur dorsalis</i>	540	534, 535
<i>Lepilemur sahamalazensis</i>	542	*
<i>Lepilemur petteri</i>	534	*
<i>Lepilemur leucopus</i>	535	19
<i>Lepilemur ruficaudatus</i>	535	103, 126, 247, 308, 533
<i>Lepilemur hubbardi</i>	535	240, 251, 268, 300
<i>Lepilemur randrianasoli</i>	538	33, 38, 270
<i>Lepilemur edwardsi</i>	545-546	137
<i>Lepilemur grawcocki</i>	544	137, 193, 355
<i>Lepilemur ahmansonii</i>	542	*
<i>Lepilemur aeeclis</i>	537-538	21, 271
<i>Lepilemur mustelinus</i>	552-553	387, 388
<i>Lepilemur jamesi</i>	552	131
<i>Lepilemur betsileo</i>	553	134, 270, 271, 284
<i>Lepilemur fleuretiae</i>	550	10, 37, 47, 198, 285, 286, 312, 315
<i>Lepilemur microdon</i>	530	25, 34, 44, 57, 107, 110, 119, 120, 121, 123, 124, 125, 135, 136, 137, 394, 552
<i>Lepilemur wrighti</i>	551	50, 54, 55, 58, 299, 474, 491
<i>Lepilemur sealii</i>	550	1, 18, 32, 54, 104, 126, 212, 218, 300

Table 3B. Summary of Population Aggregate Analysis (PAA) 12s rRNA diagnostic sites for *Lepilemur* species. Refer to Table 2B. *No Character or Attribute is available for this fragment.

Species	Fragment Size (bp)	PAA base pair location
<i>Lepilemur ankaranensis</i>	855	*
<i>Lepilemur milanoi</i>	855	498
<i>Lepilemur tynierlachsoni</i>	855	394, 693, 854
<i>Lepilemur septentrionalis</i>	855	18, 60, 110, 154, 334, 433, 488
<i>Lepilemur dorsalis</i>	855	761, 796
<i>Lepilemur sahamalazensis</i>	855	294, 766
<i>Lepilemur petteri</i>	855	240
<i>Lepilemur leucopus</i>	855	*
<i>Lepilemur ruficaudatus</i>	855	433
<i>Lepilemur hubbardi</i>	855	340
<i>Lepilemur randrianasoli</i>	855	6, 242, 369, 391, 418, 666
<i>Lepilemur edwardsi</i>	854	*
<i>Lepilemur grawcocki</i>	854	*
<i>Lepilemur ahmansonii</i>	855	413, 641, 723, 750, 768
<i>Lepilemur aeeclis</i>	855	389, 556
<i>Lepilemur mustelinus</i>	854	*
<i>Lepilemur jamesi</i>	854	66
<i>Lepilemur betsileo</i>	853	434
<i>Lepilemur fleuretiae</i>	854	53, 500, 757
<i>Lepilemur microdon</i>	855	148, 235, 270, 757, 786
<i>Lepilemur wrighti</i>	854	349, 746
<i>Lepilemur sealii</i>	855	6, 310, 469, 536, 579, 684

Table 3C. Summary of Population Aggregate Analysis (PAA) 12s rRNA diagnostic sites for Lepilemur species. Refer to Table 2C. *No Character or Attribute is available for this fragment.

Species	Fragment Size (bp)	PAA base pair location
<i>Lepilemur ankaranensis</i>	2359-2360	364, 858, 1804
<i>Lepilemur milanoii</i>	2359	342, 769, 1896
<i>Lepilemur tmyerlachsoni</i>	2359	152, 328, 1309, 1378, 1456, 1861, 1898, 1995
<i>Lepilemur septentrionalis</i>	2361	44, 113, 211, 214, 274, 353, 354, 533, 551, 555, 576, 674, 734, 1103, 1174, 1231, 1347, 1399, 1448, 1550, 1603, 1777, 2144, 2146, 2366
<i>Lepilemur dorsalis</i>	2361	579, 717, 746, 1507, 1525, 1780, 2163, 2168, 2177, 2236
<i>Lepilemur sahamalazensis</i>	2360	399, 539, 737, 749, 770, 803, 1358
<i>Lepilemur petteri</i>	2360	337, 578, 779, 957, 1615
<i>Lepilemur leucopus</i>	2360-2361	220, 448, 719, 836, 1960
<i>Lepilemur ruficaudatus</i>	2360	94, 127, 365, 667, 776, 919, 1074, 1370, 1783, 1835, 1921, 2068
<i>Lepilemur hubbardi</i>	2361	350, 543, 566, 629, 681, 1015, 1240, 1396, 1559, 1906, 1907, 2111, 2245
<i>Lepilemur randrianasoli</i>	2360	195, 397, 699, 849, 923, 1018, 1035, 1053, 1432, 1444, 1753, 1981, 1988, 2251
<i>Lepilemur edwardsi</i>	2360	856, 1108, 1194, 1343, 1474, 1979
<i>Lepilemur grewcocki</i>	2360	244, 274, 406, 629, 888, 896, 988, 1114, 1226, 1354, 1537, 2130
<i>Lepilemur ahmansonii</i>	2360	46, 304, 350, 1096, 1097, 1285, 1402, 1818, 2141, 2170
<i>Lepilemur aecclis</i>	2360	535, 548, 563, 581, 761, 975, 1357, 1368, 1423, 1442, 1480, 1990, 2089, 2107
<i>Lepilemur mustelinus</i>	2359-2360	85
<i>Lepilemur jamesi</i>	2360	140, 716, 2144
<i>Lepilemur betsileo</i>	2360	8, 1057
<i>Lepilemur fleuretae</i>	2360	29, 103, 269, 358, 533, 534, 546, 553, 664, 905, 1124, 1574, 2013, 2023
<i>Lepilemur microdon</i>	2361	146, 510, 581, 596, 826, 829, 1171, 1369, 1708, 1954, 1991
<i>Lepilemur wrighti</i>	2360	55, 133, 663, 696, 886, 871, 907, 942, 1105, 1117, 1120, 1294, 1837, 1856, 1936, 2041, 2096
<i>Lepilemur sealii</i>	2361	83, 84, 131, 166, 170, 187, 331, 409, 505, 558, 572, 615, 695, 853, 917, 937, 1045, 1228, 1235, 1270, 1332, 1348, 1421, 1423, 1453, 1548, 1795, 1921, 1939, 2056, 2153, 2178, 2179, 2296

DISCUSSION

The persistent and rapid loss of habitat and the resulting fragmentation of panmictic populations have compelled wildlife and conservation agencies to take protective action according to existing guidelines and information with the ultimate goal of prioritizing species and/or sites. The explosive rate of the deforestation in Madagascar, however, has eliminated many of the available options. Because haplotypes can be unique to each population, simply preserving one population will not necessarily maintain species-wide genetic variability. The extinction of any remnant population may not diminish the between-population variance, but may result in the permanent loss of non-neutral alleles from the composite gene pool. The loss can potentially have deleterious effects with the loss of genetic diversity

especially in primates (Pope 1996). Even if the loss of genetic diversity in primates is characterized by an overall loss of heterozygosity with most of the variation found between populations and/or social groups, the genetic loss is dependent on the proportion of the gamete pool contributed by each generation and by lineage effects (Pope 1996). The management of fragmented populations is further complicated by a lack of information, such as full extent of species distribution, from existing populations, and by the mating system and social structure of each species. Therefore, it is important to maintain the composite genetic diversity and the species reservoirs within and among these fragmented habitats.

Historically, sympatric reproductive isolation, as described in the Biological Species Concept (BSC), has been the predominant defining criteria of species status (Mayr 1942). Unfortunately, this concept is difficult to implement or delineate when the putative species in question is a geographically isolated or allopatrically defined population. In this paper, the current *Lepilemur* taxonomy was examined according to the Phylogenetic Species Concept (PSC) sensu Wheeler and Platnick et al. (2000), Louis et al. (2006), and Mayor et al. (2004). The diagnostic characters or attributes define evolutionarily significant units (ESUs). Several authors suggest that ESUs are equivalent to species as determined through the Phylogenetic Species Concept (Amato et al. 1998; Barrowclough and Flesness 1996; Cracraft 1983). The identification of eleven new species in the following descriptions establishes the essential need for extensive as well as detailed sample collections across Madagascar to determine geographic ranges for all of the sportive lemurs. The constant addition of samples to the PAA data set will continue to test the distinction of these characters.

Due to the inability to maintain sportive lemurs as long-term live vouchers in captivity, whole blood, morphometric, and e-voucher photos will serve as the type series for several of the newly described species. In each case, an attempt was also made to identify existing museum specimens to represent the type series and was listed in that section.

Lepilemur ahmansi, New Species

Type Series.—Whole blood for KIBO22 (TK125529/TTU104462), adult male; KIBO58 (TK125530/TTU104463), adult female; and KIBO65 (TK125531/TTU104464), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. KIBO22, KIBO58, and KIBO65 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantomphohavana, and John R. Zanorivelo on 23 October 2003, 27 October 2003, and 29 October 2003, respectively.

Type Locality.—MADAGASCAR, Province de Mahajanga, Tsiombikibo Classified Forest, 16°02'24.7"S, 045°48'10.6"E, and northwest of the Mahavavy River.

Description.—*L. ahmansi* is a smaller sized sportive lemur (0.61 kg) compared to *L. aeeclis* (0.86 kg) with a pelage that is primarily dark gray on the body and diffuse reddish-brown on the dorsal surface of the extremities, especially distally. They have similar color patterns to *L. aeeclis* except *L. ahmansi* lacks the prominent dorsal stripe on the dorsal midline of the back as described for *L. aeeclis* (Andriaholinirina et al. 2006). A diffuse black stripe can be present on the dorsum of the head. The ventrum is dark gray towards the midline but diffuses to a light gray ventrolaterally. The tail is primarily reddish brown, darker on the dorsal surface than the ventral portion which is a light grayish blonde.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. ahmansi* differs from the closest relative, *L. sahamalazensis*, by $5.5\% \pm 1\%$ (33 informative sites), $1.6\% \pm 0.4\%$ (13 informative sites), and $2.7\% \pm 0.3\%$ (70 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. ahmansi* differs from the closest species relative to geographic distance, *L. aeeclis*, by $9.6\% \pm 1.3\%$ (69 informative sites), $6.5\% \pm 0.8\%$ (59 informative sites), and $11.7\% \pm 0.6\%$ (282 informative sites), respectively.

Distribution.—*L. ahmansi* is currently known from the Tsiombikibo region, northwest of the Mahavavy River. The southern extent of *L. ahmansi* is unknown. Further work needs to be conducted to determine if the Maningoza, Manambaho, or Manambolo River is the southern range of *L. ahmansi* and the northern range of *L. randrianasoli*.

Comparisons and Remarks.—*L. ahmansi* is smaller in size than *L. ruficaudatus*, *L. aeeclis*, *L. randrianasoli*, and *L. edwardsi* (Table 1). Both KIBO58 and KIBO65 were adult females, supporting offspring. Although *L. ahmansi* is located geographically closer to *L. aeeclis* and *L. edwardsi*, *L. ahmansi* is taxonomically closer to the northwest sportive lemurs, *L. sahamalazensis* and *L. dorsalis* (Figures 2-6; each species is depicted by specific color throughout the fig-

ures). Additional survey work is required to determine the southern range of *L. ahmansi* and the northern extent of *L. randrianasoli*. The molecular analysis presented in this paper corroborates the phylogeographic study of Pastorini et al. (2003) and Andriaholinirina et al. (2006), with the Betsiboka River forming the southern limit of *L. edwardsi*. Further studies should be conducted north of Ankafantsika National Park to determine the northern extent of *L. edwardsi*.

Etymology.—The name *ahmansi* is proposed in honor of Robert Ahmanson and the Ahmanson Foundation who have given extensive support to the graduate programs of the Malagasy students in Madagascar and at the Henry Doorly Zoo's Center for Conservation and Research.

Vernacular Names.—Ahmanson's Sportive Lemur.

Lepilemur betsileo, New Species

Type Series.—Whole Blood for FAN11 (TK 125513/TTU104446), adult female; and FAN4.24 (TK125514/TTU104447), adult male are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. FAN11 and FAN4.24 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantomphahavana, and John R. Zaonarivelo on 28 October 2000 and 2 April 2004, respectively. According to Jenkins (1987), a specimen, ZD.1981.759 (skin and skull), is held at the British Museum of Natural History from the Ambohitombo Forest ($20^{\circ}43'S$, $047^{\circ}26'E$), which is located within the tentative range of *L. betsileo*.

Type Locality.—MADAGASCAR, Province de Fianarantsoa, Fandriana Classified Forest, (approximately $20^{\circ}23'40.5"S$, $047^{\circ}38'06.6"E$), and on the Mananjary River.

Description.—This sportive lemur is relatively large (1.11 kg) with a predominantly grayish to reddish brown color pattern. The overall pelage is a mixture

of dark to light gray and reddish brown fur, darker dorsally than ventrally. The pelage is noticeably lighter within the ear pinna bordered by dark brown to black fur along the outer edge of the anterior aspect of the pinna. The anterior portion of the mandible is white in color with the rest of the face gray in color. The tail contrasts sharply with the rest of the body, being black in color.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. betsileo* differs from its closest relatives by both genetic and geographic distance, *L. mustelinus* and *L. microdon*, by $5.2\% \pm 0.9\%$ (42 informative sites) and $11.5\% \pm 1.3\%$ (76 informative sites), $0.7\% \pm 0.2\%$ (9 informative sites) and $6.8\% \pm 0.8\%$ (60 informative sites), and $2.2\% \pm 0.2\%$ (67 informative sites) and $15.7\% \pm 0.8\%$ (370 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. betsileo* differs from another new species, *L. jamesi*, by $5.8\% \pm 1\%$ (34 informative sites), $1\% \pm 0.3\%$ (8 informative sites), and $1.8\% \pm 0.2\%$ (41 informative sites), respectively.

Distribution.—*L. betsileo* is currently known from the Fandriana region, between the Mangoro and Namorona Rivers. The southern and northern distribution of *L. betsileo* is unknown and further work needs to be conducted to confirm the extent of its range.

Comparisons and Remarks.—*L. betsileo* is intermediate in size to *L. mustelinus* and *L. microdon* (Table 1). FAN11 was an adult female, supporting an offspring. *L. betsileo* is located geographically closest to *L. microdon* to the southeast and *L. mustelinus* to the north (Figures 2-6). Additional survey work is required to confirm the southern and northern ranges of *L. betsileo*. The range of *L. microdon* appears to extend in a northeast to southwest trajectory from Ranomafana National Park to Andringitra National Park. The southern limit of *L. betsileo* most likely is the Namorona River.

Etymology.—The name *betsileo* is proposed for this species and is derived from the Malagasy tribe from the Fianarantsoa region.

Vernacular Names.—Betsileo Sportive Lemur.

Lepilemur fleuretae, New Species

Type Series.—Whole blood for AND20 (TK125559/TTU104492), adult male, is stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the TTU catalog number. AND20 was collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Edward Louis on 12 May 2004.

Type Locality.—MADAGASCAR, Province de Toliary, Manangotry, Andohahela National Park (approximately 24°45'46.0"S, 046°51'47.0"E).

Description.—This sportive lemur is medium-sized (0.80 kg) with predominantly gray pelage, with a grayish-brown mixture along the proximal portion of the extremities. The pelage is noticeably lighter over the eyelids from the rest of the face. Running along the midline, a diffus stripe is present, starting from the forehead and continuing approximately halfway down the back. The venter is a lighter brownish gray with some light brown along the lateral edges of the belly. The tail is reddish gray proximally, becoming darker gray towards the tip.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. fleuretae* differs from its closest relative by genetic distance, *L. mustelinus*, by $7.7\% \pm 1.0\%$ (59 informative sites), $1.5\% \pm 0.4\%$ (19 informative sites), and $4.5\% \pm 0.4\%$ (177 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. fleuretae* differs from its closest relatives by both geographic and genetic distance from two other new species, *L. jamesi* and *L. wrighti*, by $7.6\% \pm 1.1\%$ (44 informative sites) and $10.2\% \pm 1.2\%$ (70 informative sites), $1.9\% \pm 0.5\%$ (18 informative sites) and $3.1\% \pm 0.5\%$ (27 informative sites), and $4.3\% \pm 0.7\%$ (113 informative sites) and $7.6\% \pm 0.6\%$ (187 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. fleuretae* differs from its closest relative by geographic distance, *L. leucopus*, by $14.1\% \pm 1.5\%$ (92 informative sites), $7.0\% \pm 0.9\%$ (62 informative sites), and $16.9\% \pm 0.8\%$ (409 informative sites), respectively.

Distribution.—*L. fleuretae* is currently known from the Manangotry region, the rainforest parcel of Andohahela National Park between the Mandrare River to the west and the Mananara River to the north (Figure 8). The southern and northern distribution of *L. fleuretae* is confined to the rain forest within the boundaries of the Mandrare and Mananara Rivers. Further work needs to be conducted to confirm the extent of its range.

Comparisons and Remarks.—*L. fleuretae* is approximately the same size as *L. jamesi*, but is smaller than *L. mustelinus* and *L. wrighti* (Table 1). *L. fleuretae* is the most genetically divergent of all of the southeastern *Lepilemur* species with the exception of *L. wrighti* and *L. microdon* (Figures 2–8). The type series of *L. microdon* is located south of Fianarantsoa which sets the distribution of this recognized species at Ranomafana National Park (Andriaholinirina et al. 2006; Petter et al. 1977; Figure 8). Genetically, *L. fleuretae* is within the *L. mustelinus* clade representing the east coast *Lepilemur* group, whereas *L. microdon* is closely related to *L. edwardsi*, an east coast sportive lemur (Figures 2–7). Further studies should be conducted north of Manangotry to confirm the northern extent of *L. fleuretae* (Figure 8).

Etymology.—The name *fleuretae* is proposed in honor of Madame Fleurete Andriantsilavo, former Secrétaire Général du MINENVEF. Madame Fleurete worked tirelessly and constantly strove for the long term conservation of Madagascar's protected and unprotected areas.

Vernacular Names.—Fleurete's Sportive Lemur.

Lepilemur grawcocki, New Species

Type Series.—Whole blood for HIH21 (TK125519/TTU104452), adult male; HIH22 (TK125520/TTU104453), adult female; and HIH23 (TK125521/TTU104454), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. HIH21,

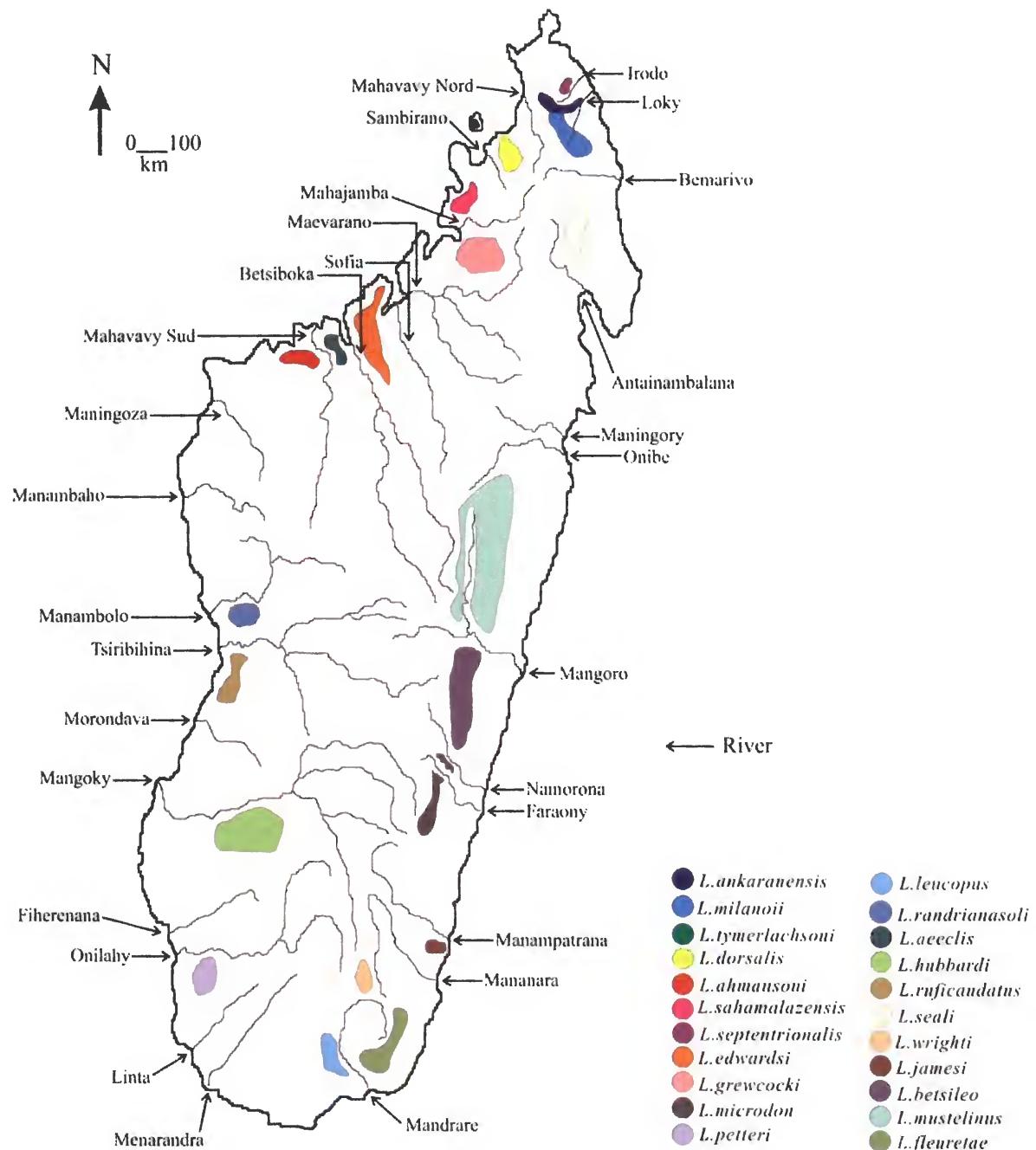


Figure 8. Proposed distribution of the sportive lemurs of Madagascar.

HIH21, HIH22, and HIH23 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantompohavana, and John R. Zaonarivelo on 13 November 2004.

Type Locality.—MADAGASCAR, Province de Mahajanga, Anjiamangirana Classified Forest (approximately 15°09'14.9"S, 047°43'41.0"E).

Description.—*L. grawcocki* is a medium-sized sportive lemur (0.78 kg) with a predominantly gray color pattern. The area around the mandible and the dorsal surface of the snout is whitish-pink in coloration. A dark stripe is present on the dorsal midline surface of the head. This black stripe may continue dorsally onto the back, but this character is individually variable. The venter is light gray to white. Unlike *L. edwardsi*, which has a consistently white tipped tail, the tail of *L. grawcocki* is entirely gray.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. grawcocki* differs from its closest relative by genetic distance, *L. edwardsi*, by 5.3%±1.0% (35 informative sites), 0.8%±0.3% (8 informative sites), and 2.8%±0.3% (66 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. grawcocki* differs from its closest relatives by geographic distance, *L. sahamalazensis*, by 6.8%±1.1% (51 informative sites), 4.8%±0.7% (40 informative sites), and 9.9%±0.6% (239 informative sites), respectively.

Distribution.—*L. grawcocki* currently is known from the Anjiamangirana region, south of the Mahajamba River and north of the Maevarano and Sofia Rivers.

Comparisons and Remarks.—*L. grawcocki* (0.78 kg) is smaller than *L. edwardsi* (1.10 kg), and larger than *L. sahamalazensis* (0.70 kg). Although *L. grawcocki* is located closer geographically to *L. sahamalazensis*, *L. grawcocki* is taxonomically more closely related to the western sportive lemur, *L. edwardsi*, and southeastern sportive lemur, *L. microdon* (Figures 2–6). Further studies should be conducted north of Ankafantsika National Park to determine the northern extent of *L. edwardsi*, and south of Anjiamangirana to determine the southern extent of *L. grawcocki* (Figure 8).

Etymology.—The name *grawcocki* is proposed in honor of Bill and Berniece Grawcock who have generously supported our fieldwork in Madagascar and provided the laboratories and housing for all of the Malagasy graduate students in Omaha. The Grawcock's support is instrumental, transferring conservation related technology to the future Malagasy scientists.

Vernacular Names.—Grawcock's Sportive Lemur.

Lepilemur hubbardi, New Species

Type Series.—Whole blood for ZOMB9 (TK125558/TTU104491), adult female; ZOMB12 (TK125556/TTU104489), adult male; and ZOMB15 (TK125557/TTU104490), adult male; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. ZOMB9, ZOMB12, and ZOMB15 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Rambinintsoa Andriantompohavana on 15 March 2004, 15 March 2003, and 16 March 2003, respectively.

Type Locality.—MADAGASCAR, Province de Toliary, Zombitse National Park (approximately 22°53'18.7"S, 044°41'43.3"E).

Description.—*L. hubbardi* is a large-sized sportive lemur (0.99 kg) with reddish-brown, gray, and white pelage. The face is grayish-brown around the muzzle and eyes with a reddish-brown dorsal surface crown. The fur around the neck is lighter, forming a reddish blonde collar. The dorsum is dark reddish-brown around the shoulders and upper back, gradually becoming a lighter reddish-white to gray towards the base of the tail and hips. The venter is entirely white. The tail is uniformly reddish blonde.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. hubbardi* differs from its closest relative by geographic and genetic distance, *L. ruficaudatus*, by 6.4%±1% (41 informative sites), 1.4%±0.4% (15 informative sites), and 3.5%±0.3% (141 informative sites), respectively.

Distribution.—*L. hubbardi* is currently only known from the Zombitse National Park region, north of the Onilahy River and south of the Mangoky River.

Comparisons and Remarks.—*L. hubbardi* (0.99 kg) is larger in size than *L. ruficaudatus* (0.86 kg). Two phenotypes have been seen in Zombitse National Park. Currently, the sample size is too small to categorically determine if the phenotypes are sexually dichromatic. Additional survey work is required to determine the southern range of *L. hubbardi* and the northern extent of *L. ruficaudatus* (Figure 8).

Etymology.—The name *hubbardi* is proposed in honor of Theodore F. and Claire M. Hubbard Family Foundation for their generous support of Malagasy graduate students in the field and in the laboratory at Henry Doorly Zoo's Center for Conservation and Research (CCR). By providing the new laboratory and housing for the CCR's Genetics Department, the Hubbard Family Foundation's support will continue to be instrumental in transferring conservation related technology to the future Malagasy scientists.

Vernacular Names.—Hubbard's Sportive Lemur.

Lepilemur jamesi, New Species

Type Series.—Whole blood for M140 (TK125538/TTU104471), adult male; M141 (TK125539/TTU104472), adult male; and M142 (TK125540/TTU104473), adult male; are stored and curated at Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. M140, M141, and M142 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, John R. Zaonarivel, and Edward Louis on 13 November 2000.

Type Locality.—MADAGASCAR, Province de Fianarantsoa, Manombo Special Reserve (approximately 23°01'69.5"S, 047°43'84.1"E).

Description.—*L. jamesi* is a large sized sportive lemur with primarily brown pelage. The face is demarcated into a mask, with whitish gray marking

along the jaw and throat from the chin to the ears. The dorsum of the head is brown with a black midline which is continuous for almost the entire length of the body. The dorsal region of the large cupped shaped ears is gray with the borders edged with black. There is usually a small cream colored patch restricted to the region beneath the ears. The venter is primarily brown, but a lighter shade than the dorsal pelage. Grayish-brown pelage is found around the ventral surface of the extremities and belly. The tail is brown proximally, gradually becoming a darker brown to black distally. The pelage is shorter than *L. fleuretae* and *L. betsileo*, giving the smooth appearance to the coat.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. jamesi* differs from its closest relatives (two newly described species) by geographic and genetic distance, *L. betsileo* and *L. fleuretae*, by $5.8\% \pm 1\%$ (34 informative sites) and $7.6\% \pm 1.1\%$ (44 informative sites), $1\% \pm 0.3\%$ (8 informative sites), and $1.8\% \pm 0.2\%$ (41 informative sites) and $4.3\% \pm 0.7\%$ (113 informative sites), respectively.

Distribution.—*L. jamesi* is currently known from Manombo Special Reserve region, south of the Manampatrana River and north of the Mananara River.

Comparisons and Remarks.—*L. jamesi* (0.78 kg) is approximately the same size as *L. fleuretae* (0.80 kg), but *L. jamesi* is smaller than *L. betsileo* (1.11 kg). Additional survey work is required to determine the precise southern and northern range of *L. jamesi* (Figure 8). These two rivers already act as barriers for two other species, “pure” *Eulemur albocollaris* and a proposed species of *Microcebus* (Louis et al. 2006; Mittermeier et al. 2006). *L. jamesi* is found in one of the few remaining low altitude, coastal, rain forests.

Etymology.—The name *jamesi* is proposed in honor of the Larry, Jeannette, and Barry James' Family for their generous and long term support of Malagasy graduate students in the field and in the laboratory at Henry Doorly Zoo's Center for Conservation and Research.

Vernacular Names.—James' Sportive Lemur.

***Lepilemur milanoii*, New Species**

Type Series.—Whole blood for DAR4.7 (TK125516/TTU104449), adult female; DAR4.17 (TK125517/TTU104450), adult male; and DAR4.18 (TK125564/TTU104497), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. DAR4.7, DAR4.17, and DAR4.18 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Edward Louis on 25 November 2004, 26 November 2004, and 26 November 2004, respectively. DAR5.1, adult male; and DAR5.2, female, are live vouchers maintained at Parc Botanique et Zoologique de Tsimbazaza; 2 x 2.0 mm biopsies from ear pinna and 1.0 cc of whole blood; tissues stored at Henry Doorly Zoo's Center for Conservation and Research. A Microchip pit tag was placed subcutaneously between scapulae of DAR5.1 and DAR5.2 and recorded as 462C010E43 and 46506B0114, respectively. DAR5.1 and DAR5.2 were collected by Richard Randriamampionona, Gerard Nalanirina, and John R. Zaonarivelo on 18 October 2005. Complete measurements are available in Appendix Ia.

Type Locality.—MADAGASCAR, Province de Antsiranana, Daraina, Andranotsimaty (approximately 13°08'52.5"S, 049°41'11"E).

Description.—*L. milanoii* is reddish-brown on back and grayish-white on the venter. The head is reddish-brown dorsally, but gray brown on the face, forming a mask appearance. A diffuse darker brown midline stripe is found on the dorsum of the head, continuing partially down the back. The anterior portion of the thighs is reddish-brown, but the majority of the limbs are gray in color. The pelage is long and thick, and missing portions of the pelage, especially on the posterior limbs prominently gray, contrasting from the reddish-brown surrounding fur. The tail is uniformly reddish-brown.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. milanoii* differs from its closest relatives by geographic and genetic distance, *L. ankaranensis*, *L. septentrionalis*, and *L. dorsalis*,

by $2.7\% \pm 0.6\%$ (20 informative sites), $5.9\% \pm 1\%$ (38 informative sites), and $5.1\% \pm 0.9\%$ (39 informative sites); $1.9\% \pm 0.4\%$ (18 informative sites), $4.4\% \pm 0.6\%$ (38 informative sites), and $2.9\% \pm 0.5\%$ (25 informative sites); and $1.2\% \pm 0.2\%$ (33 informative sites), $8.4\% \pm 0.5\%$ (198 informative sites), and $4.2\% \pm 0.3\%$ (100 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. milanoii* differs from another species that is geographically close and newly described, *L. tmyerlachsoni*, by a genetic distance of $2.5\% \pm 0.6\%$ (18 informative sites), $2.1\% \pm 0.5\%$ (18 informative sites), and $2.3\% \pm 0.3\%$ (54 informative sites), respectively.

Distribution.—*L. milanoii* is currently known from the Daraina region, south of the Loky River. *L. milanoii* has been identified with molecular data in Andrafiamena Classified Forest. *L. ankaranensis* has also been identified at Andrafiamena Classified Forest.

Comparisons and Remarks.—*L. milanoii* (0.72 kg) is approximately the same size as *L. dorsalis* (0.73 kg), smaller than *L. ankaranensis* (0.79 kg), but larger than *L. septentrionalis* (0.6 kg). Although *L. milanoii* has been identified within the range of *L. ankaranensis* at Andrafiamena Classified Forest, *L. milanoii* is the only species found at Daraina. Additionally, *L. milanoii* has not been found at Ankarana or Analamera National Parks which has only *L. ankaranensis*. The Loky River is currently the northern barrier for *Propithecus tattersalli*, but *L. milanoii* has managed to cross this barrier, probably towards the river's source when there was an intact forest track between Daraina and Andrafiamena (Figure 8). Further studies should be conducted south of Andrafiamena Classified Forest and the southwestern limit of the Loky River to determine the distribution of *L. milanoii*. Additionally, extensive population studies should be conducted at Andrafiamena Classified Forest to determine the population dynamics of the two species found there.

Etymology.—The name *milanoii* is proposed for the Daraina region and is derived from the Malagasy language and means, “to swim”. The Malagasy people refer to the Daraina region as “Daraina milanoa” which means “Daraina swimming” in reference to their swimming in the Andranotsimaty River looking for gold.

Vernacular Names.—Daraina or Swimming Sportive Lemur.

Lepilemur petteri, New Species

Type Series.—Whole blood for BEZ15 (TK125511/TTU104444), adult female; BEZ18 (TK125563/TTU104496), adult male; and BEZ21 (TK125512/TTU104445), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. BEZ15, BEZ18, and BEZ21 were collected by Richard Randriamampionona and Edward Louis on 5 March 2001, 5 March 2001, and 6 March 2001, respectively. According to Jenkins (1987), a specimen, ZD.1892.111.61, (skull) is held at the British Museum of Natural History from the Ambolisatra Forest ($23^{\circ}03' S$, $043^{\circ}24' E$) which is located within the tentative range of *L. petteri*.

Type Locality.—MADAGASCAR, Province de Toliary, Beza-Mahafaly (approximately $23^{\circ}39'11.4'' S$, $044^{\circ}37'90.6'' E$).

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. petteri* differs from its closest relative by geographic and genetic distance, *L. leucopus*, by $3.4\% \pm 0.8\%$ (21 informative sites), $1.1\% \pm 0.3\%$ (9 informative sites), and $1.8\% \pm 0.2\%$ (46 informative sites), respectively.

Distribution.—*L. petteri* is currently known from the Beza-Mahafaly region, south of the Onilahy River and west of the Linta and Menarandra Rivers.

Description.—*L. petteri* is larger than *L. leucopus* with a similar gray to grayish-brown body (Table 1). The venter is whitish-gray. The face is gray with lighter circular patches around the eyes and under the chin. The ears are trimmed in lighter fur with the anterior or inner lining of the ear dark brownish-gray which highlights the ear. There is diffuse brownish-gray pelage on the anterior aspect of the thigh and along the dorsal midline.

Comparisons and Remarks.—*L. petteri* (0.63 kg) is larger than *L. leucopus* (0.54 kg). *L. petteri* is

located in primarily deciduous thicket or thorn scrub (spiny) and in the limited gallery forests. *L. leucopus* is found in the spiny desert forest parcels of Andohahela National Park. Further studies should be conducted north of Onilahy River to determine the northern extent of *L. petteri*. Additionally, further studies should be conducted in the remaining forest regions around the Linta and Menarandra Rivers to determine the distribution of both *L. petteri* and *L. leucopus* (Figure 8).

Etymology.—The name *petteri* is proposed in honor of Jean-Jacques Petter for his immense body of work on lemurs, including the sportive lemurs. Considered a leader in French Primatology, Dr. Petter was a winner of the WWF Gold Medal in 1981 for his conservation work in Madagascar.

Vernacular Names.—Petter's Sportive Lemur.

Lepilemur sealii, New Species

Type Series.—Whole blood for JAR2 (TK125523/TTU104456), adult male; JAR3 (TK125524/TTU104457), adult female; and JAR8 (TK125525/TTU104458), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. JAR2, JAR3, and JAR8 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, and Edward Louis on 19 July 2001, 19 July 2001, and 21 July 2001, respectively.

Type Locality.—MADAGASCAR, Province de Antsiranana, Anjanaharibe-Sud Special Reserve (approximately $14^{\circ}47'45.1'' S$, $049^{\circ}27'88.5'' E$).

Description.—*L. sealii* is a large-sized sportive lemur (0.95 kg) with a uniform light chocolate-brown to reddish-brown color pattern. The venter is lighter brownish-gray and the pelage is extremely long and thick throughout the body. The face is light brownish-gray and is uniform in color. The hands and feet are a lighter grayish-brown. The tail, in contrast to the rest of the body, is brownish-gray throughout its length.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. sealii* differs from its closest relative by genetic distance, *L. mustelinus*, by $10.1\% \pm 1.1\%$ (70 informative sites), $4.4\% \pm 0.6\%$ (43 informative sites), and $10.7\% \pm 0.6\%$ (274 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. sealii* differs from its closest relatives by geographic distance, *L. wrighti*, a newly described species found at Kalambatitra Special Reserve, by $9.2\% \pm 1.1\%$ (79 informative sites), $4.3\% \pm 0.6\%$ (37 informative sites), and $10.1\% \pm 0.5\%$ (242 informative sites), respectively.

Distribution.—*L. sealii* is currently known from the Anjanaharibe-Sud region, north of the Antainambalana River.

Comparisons and Remarks.—*L. sealii* (0.95 kg) is approximately the same size as *L. mustelinus* (0.99 kg) and *L. wrighti* (0.95 kg). Although *L. sealii* is located closer geographically to *L. mustelinus*, *L. sealii* is taxonomically closer related to the southeastern sportive lemur, *L. wrighti* (Figures 2–8). Additional survey work is required to determine the southern range of *L. sealii* and the northern extent of *L. mustelinus*. Currently, we have assigned the sportive lemur from Mananara-Nord (south of the Antainambalana River) to *L. sealii* even though the available molecular data suggests that this population will be described as a separate species in the future, pending further field studies. Further studies also should be conducted north of Anjanaharibe-Sud Special Reserve to determine the northern extent of *L. sealii* (Figure 8).

Etymology.—The name *sealii* is proposed in honor of Dr. Ulysses Seal, an architect of the Conservation Breeding Specialist Group SSC/IUCN, and a definitive leader, teacher, and motivator of in situ conservation throughout the world.

Vernacular Names.—Seal's Sportive Lemur.

Lepilemur tymerlachsoni, New Species

Type Series.—Whole blood for LOKO4.2 (TK125535/TTU104468), adult male; LOKO4.5 (TK125537/TTU104470), adult female; and LOKO4.33

(TK125536/TTU104469), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix Ia) and from The Museum of Texas Tech University under the respective TTU catalog numbers. LOKO4.2, LOKO4.5, and LOKO4.33 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantomphohavana, and John R. Zaonarivelo on 6 July 2004, 6 July 2003, and 9 July 2004, respectively.

Type Locality.—MADAGASCAR, Province de Antsiranana, Nosy Be, Lokobe National Park (approximately $13^{\circ}23'27.6''S$, $048^{\circ}18'15.2''E$).

Description.—*L. tymerlachsoni* is light brownish-gray with the upper half of the back a lighter reddish-brown. The venter is a light grayish-white. The anterior aspects of the thighs and edges of the extremities also have a light reddish-brown diffuse color. A dark brown to black midline dorsal stripe is present from the head to the lower half of the back. The face is gray with the appearance of a mask. The tail is an uniform light reddish-gray to brown.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. tymerlachsoni* differs from its closest relatives by both genetic and geographic distance, *L. milanoii*, *L. ankaranensis*, *L. dorsalis*, and *L. sahamalazensis*, by $2.5\% \pm 0.6\%$ (18 informative sites), $3.9\% \pm 0.8\%$ (25 informative sites), $4.9\% \pm 1\%$ (33 informative sites), and $4.4\% \pm 0.9\%$ (30 informative sites); $2.1\% \pm 0.5\%$ (18 informative sites), $2.2\% \pm 0.5\%$ (20 informative sites), $2.2\% \pm 0.5\%$ (18 informative sites), and $2.5\% \pm 0.5\%$ (20 informative sites); $2.3\% \pm 0.3\%$ (54 informative sites), $2.3\% \pm 0.3\%$ (55 informative sites), $4.7\% \pm 0.4\%$ (110 informative sites), and $4.8\% \pm 0.4\%$ (126 informative sites), respectively.

Distribution.—*L. tymerlachsoni* is currently known from the Lokobe region and Nosy Be Island.

Comparisons and Remarks.—*L. tymerlachsoni* (0.88 kg) is larger than *L. milanoii* (0.72 kg), *L. sahamalazensis* (0.70 kg), *L. dorsalis* (0.73 kg), *L. ankaranensis*, and *L. septentrionalis* (0.60 kg). Andria-

holinirina et al. (2006) presented data that distinguished *L. sahamalazensis* from *L. dorsalis* (Ambanja/Nosy Be), but the morphological and molecular data clearly separate *L. dorsalis* (Manongarivo/Antafondro) and *L. tmymerlachsoni* (Nosy Be), and is comparable to differences between the other northern recognized sportive lemurs (Figures 2-8).

Etymology.—The name *tmymerlachsoni* is proposed in honor of the Howard and Rhonda Hawk Family who have made generous contributions to the Madagascar Project, providing infra-structure and field support to the many Malagasy graduate students.

Vernacular Names.—Hawk's Sportive Lemur.

Lepilemur wrighti, New Species

Type Series.—Whole blood for KALA4.9 (TK125527/TTU104460), adult female; KALA4.16 (TK125565/TTU104498), adult male; and KALA4.18 (TK125526/TTU104459), adult female; are stored and curated at The Museum of Texas Tech University. Individual measurements, e-voucher photos, and collection data are available online (see Appendix 1a) and from The Museum of Texas Tech University under the respective TTU catalog numbers. KALA4.9, KALA4.16, and KALA4.18 were collected by Richard Randriamampionona, Jean C. Randriamanana, Gerard Nalanirina, Rambinintsoa Andriantomphohavana, and Edward Louis on 12 June 2004, 12 June 2003, and 14 June 2004, respectively.

Type Locality.—MADAGASCAR, Province de Toliary, Kalambatritra Special Reserve, Befarara (approximately 23°25'05.4"S, 046°26'55.4"E).

Description.—*L. wrighti* is a large-sized lemur with a diffuse reddish-brown and gray pelage. The dorsum is reddish-brown to grayish-brown. The venter is grayish-brown, lighter in color than the dorsum. The head of females is uniformly gray, sharply contrasting with the rest of the body. The males have a diffuse reddish brown to gray appearance that does not contrast dramatically with the body. Thus, based on our limited sample size ($n = 5$), *L. wrighti* represents the first instance of sexual dichromatism in the genus *Lepilemur*. Furthermore, in some individual females, there is a slight color change around the face that forms

a mask-like appearance. For both sexes, the ears have minimal to short fur and are lighter in color.

Diagnosis.—In the D-loop, 12s rRNA, and PAST sequence fragments, *L. wrighti* differs from its closest relatives by genetic distance, *L. seali* and *L. fleuretae*, by $9.2\% \pm 1.1\%$ (79 informative sites) and $10.2\% \pm 1.2\%$ (70 informative sites); $4.3\% \pm 0.6\%$ (37 informative sites) and $3.1\% \pm 0.5\%$ (27 informative sites); and $10.1\% \pm 0.5\%$ (242 informative sites) and $10.8\% \pm 0.5\%$ (187 informative sites), respectively. In the D-loop, 12s rRNA, and PAST sequence fragments, *L. wrighti* differs from its closest relative geographically, *L. leucopus*, by genetic distance of $13.9\% \pm 1.4\%$ (99 informative sites), $3.1\% \pm 0.5\%$ (27 informative sites), and $16.4\% \pm 0.8\%$ (395 informative sites), respectively.

Distribution.—*L. wrighti* is currently known from Kalambatritra Special Reserve, west of the Mananara River and north of the Mandrare River.

Comparisons and Remarks.—*L. wrighti* (0.95 kg) is a large sized sportive lemur, approximately the same size as *L. mustelinus* (0.99 kg), but larger than *L. fleuretae* (0.80 kg). With its close taxonomic relationship with the northeastern sportive lemur, *L. seali*, and its distinctive morphological appearance, the species is well differentiated from other sportive lemurs in eastern Madagascar. Further studies need to be conducted to determine its distribution (Figure 8) and to verify the possible pelage difference between males and females.

Etymology.—The name *wrighti* is proposed in honor of Dr. Patricia Wright for her long term dedication and contributions to conservation in Madagascar and tropical environments throughout the world.

Vernacular Names.—Wright's Sportive Lemur.

As with all of the lemur taxa of Madagascar, comprehensive census and taxonomic studies of free-ranging populations in the Genus *Lepilemur* are necessary for the implementation of management and conservation programs. The existing distribution records for all of the *Lepilemur* species are limited (Thalmann and Ganzhorn 2003). Furthermore, the molecular data from previous studies regarding multiple lemur species reflects specific biases to regions of

the mitochondrial DNA; and therefore, data sets based on independent vouchers or sample sets are difficult to correlate (Andriaholinirina et al. 2006; Pastorini et al. 2003; Wyner et al. 1999; Yoder et al. 2000). Although the sequence data presented in this paper are not all-inclusive nor equivalent to every lemur mtDNA study or region, the authors for the first time present sequence data from three regions of the mtDNA in an attempt to submit not only new data, but also to correlate the data with previous studies. By developing an equivalent data set with respect to the various regions of the mtDNA sequenced by the various researchers, a comprehensive and cumulative approach could be created that would link independent but complementary research programs.

The processes of evolution are an important component of species concepts, science, and investigation. The PSC not only encompasses a cladistic perspective, but also allows the biologist to focus operationally on the results of evolution to present and to delineate species. A cumulative approach implementing morphological, cytogenetic, and molecular data would be the ideal approach when defining species (Mayor et al. 2004; Mittermeier et al. 2006). The fine-tuning of dynamic population studies will require constant and consistent addition of nuclear and mitochondrial DNA data from multiple individuals from all geographic ranges to this data set. Results derived from such a data set would be instrumental in making accurate, precise, and responsible management decisions by wildlife and conservation entities.

By applying the phylogeographic studies by Pastorini et al. (2003) and Thalmann (2000), geographic barriers can be defined that affect multiple taxa, including both flora and fauna. By establishing and prioritizing these phylogeographic regions, conservation management decisions can be implemented that will support the preservation of biodiversity within these critically

defined regions. Superimposition of the new *Lepilemur* species' distributions on a geophysical map indicates that the rivers are forming significant barriers, contributing to the processes of speciation. Additionally, an inverse relationship appears to exist between body size and number of species with the smaller body sized genera containing the greater number of species. This effect appears to be more amplified in the nocturnal lemurs which have smaller territories than the larger bodied diurnal lemurs, with rivers forming the limiting boundaries for each species. The eastern *Lepilemur* species also appear to have less dense populations than the species found in northern and western Madagascar. Correlating *Microcebus* and *Avahi* sequence data to the distributions of the 22 *Lepilemur* species, a geophysical map is created which indicates a comparative partitioning based on unique species, with their distributions bounded by the same river systems or pairs (unpublished data; Louis et al. 2006). The known distributions of the mid-sized diurnal lemurs, for example, the Genus *Eulemur*, also corresponds to the *Lepilemur* species distributions. Even a cursory glance at the geophysical map and the distributions of the 22 sportive lemurs, allows researchers to predict areas where new species likely exist; therefore, more effectively concentrating research efforts (Figure 8).

The extreme degree of regional endemism, the continued risk from human encroachment, and the restricted geographic ranges combined with the inadequate knowledge of established distributions of described lemurs across Madagascar, emphasizes the need for further investigations in unexplored sites and the re-evaluation of protective measures, conservation ranking, and management of these species. The limited knowledge of geographic limits should be a major priority for conservationists and scientists alike.

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LITERATURE CITED

Amato, G., J. Gatesy, and P. Brazaitis. 1998. PCR assays of variable nucleotide sites for identification of conservation units: an example from *Caiman*. Pp. 177-190 in Molecular approaches to ecology and evolution (R. DeSalle and B. Schierwater, eds.). Birkhäuser Verlag, Basel, Switzerland.

Andriaholinirina, N., J-L. Fausser, C. Roos, C. Rabarivola, I. Ravarimanana, D. Zinner, U. Thalmann, J. U. Ganzhorn, B. Meier, R. Hilgartner, L. Walter, A. Zaramody, C. Langer, T. Hahn, E. Zimmermann, U. Radespiel, M. Craul, J. Tomiuk, I. Tattersall, and Y. Rumpler. 2006. Molecular phylogeny and taxonomic revision of the sportive lemurs (*Lepilemur*, Primates). BioMed Central Evolutionary 6:1-13.

Baker, C. S., A. Perry, J. L. Bannister, M. T. Weinrich, R. B. Abernethy, J. Calambokidis, R. H. Lien, J. U. Lambersen, O. Ramirez, P. Vasquez, J. Clapham, A. Alling, S. J. O'Brien, and S. R. Palumbi. 1993. Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. Proceedings of the National Academy of Sciences 90:8239-8243.

Bandelt, H-J, P. Forster, and A. Röhl. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37-48.

Barrowclough, G. F., and N. R. Flesness. 1996. Species, subspecies, and races: the problem of units of management in conservation. Pp. 247-254 in Wild mammals in captivity (G. G. Kleiman, M. Allen, and H. Harris, eds.). University of Chicago Press, Chicago, Illinois.

Cracraft, J. 1983. Species concepts and speciation analysis. Pp. 159-187 in Current ornithology, Vol. 1 (R. F. Johnston, ed.). Plenum Press, New York.

Davis, J. I., and K. C. Nixon. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. Systematic Biology 41:421-435.

Felsenstein, J. 2005. PHYLIP (Phylogeny Inference Package) version 3.6. Distributed by author. Department of Genome Sciences, University of Washington, Seattle.

Forster, P., A. Torroni, C. Renfrew, and A. Röhl. 2001. Phylogenetic star contraction applied to Asian and Papuan mtDNA evolution. Molecular Biology and Evolution 18:1864-1881.

Geng, H., D. Bastola, and H. Ali. 2004. A new approach to clustering biological data using message passing. Proceedings of the 2004 IEEE Computational Systems Bioinformatics Conference 2004:493-494.

Geng, H., X. Deng, D. Bastola, and H. Ali. 2005. On clustering biological data using unsupervised and semi-supervised message passing. Proceedings of the 5th IEEE Symposium on Bioinformatics and Bioengineering 2005:294-298.

Gonzales, S., J. E. Maldonado, and J. A. Leonard. 1998. Conservation genetics of the endangered pampas deer (*Ozotoceros bezoarticus*). Molecular Ecology 7:47-57.

Groves, C. P. 2000. The Genus *Cheirogaleus*: unrecognized biodiversity in dwarf lemurs. International Journal of Primatology 21:943-961.

Groves, C. P. 2001. Primate taxonomy. Smithsonian Institution, Washington, D.C.

Hedges, S. B. 1994. Molecular evidence for the origin of birds. Proceedings of the National Academy of Sciences 91:2621-2624.

Huelsenbeck, J. P., and F. Ronquist. 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17:754-755.

Ishak, B., S. Warter, B. Butrillaux, and Y. Rumpler. 1992. Chromosomal rearrangements and speciation of sportive lemurs (*Lepilemur* species). Folia Primatologica 58:121-130.

IUCN/SSC Criteria Review Working Group. 1999. IUCN Red List Criteria review provisional report: draft of the proposed changes and recommendations. Species 31-32:43-57.

Jenkins, P. D. 1987. Catalogue of primates in the British Museum (Natural History) and elsewhere in the British Isles. Part IV: suborder Strepsirrhini, including the subfossil Madagascan lemurs and Family Tarsiidae. British Museum (Natural History), London, England.

Jernvall, J., and P. C. Wright. 1998. Diversity components of impending primate extinctions. Proceedings of the National Academy Sciences 95:11279-11283.

Kappeler, P. M., R. M. Rasololiarison, L. Razafimanantsoa, L. Walter, and C. Roos. 2005. Morphology, behaviour and molecular evolution of giant mouse lemurs (*Mirza* spp.) Gray, 1870. with description of a new species. Primate Report 71:3-26.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16:111-120.

Kumar, S., K. Tamura, and M. Nei. 1993. MEGA: Molecular Evolutionary Genetics Analysis, Version 2.1. Pennsylvania State University, University Park Press, Baltimore, Maryland.

Longmire, J. L., G. F. Gee, C. L. Hardekoff, and G. A. Mark. 1992. Establishing paternity in whooping cranes (*Grus americana*) by DNA analysis. *The Auk* 109:522-529.

Louis, E. E. Jr., M. S. Coles, R. Andriantompohavana, J. A. Sommer, S. E. Engberg, J. R. Zaonarivelo, M. I. Mayor, and R. A. Brenneman. 2006. Revision of the mouse lemurs (*Microcebus*) of eastern Madagascar. *International Journal of Primatology* 27:347-389.

Maddison, W. P., and D. R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution. Sinauer Associates, Sunderland, Massachusetts.

Martin, R. D. 2000. Origins, diversity, and relationships of lemurs. *International Journal of Primatology* 21:1021-1049.

Mayor, M. I., J. A. Sommer, M. L. Houck, J. R. Zaonarivelo, P. C. Wright, C. Ingram, S. R. Engel, and E. E. Louis, Jr. 2004. Specific status of *Propithecus* spp. *International Journal of Primatology* 25:875-900.

Mayr, E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. Columbia University Press, New York.

Mittermeier, R. A., I. Tattersall, W. R. Konstant, D. M. Meyers, and R. B. Mast. 1994. Sportive lemurs. Pp. 83-94 in *Lemurs of Madagascar*. Conservation International, Washington, D. C.

Mittermeier, R. A., W. R. Konstant, F. Hawkins, E. E. Louis, O. Langrand, J. Ratsimbazafy, R. Rasoloarison, J. U. Ganshorn, S. Rajaobelina, I. Tattersall, and D. M. Meyers. 2006. Sportive lemurs. Pp. 183-208 in *Lemurs of Madagascar*, 2nd Edition. Conservation International Tropical Field Guide Series, Washington, D. C.

Montagnon, D., I. B. Ravaoarimanana, and Y. Rumpler. 2001. Taxonomic relationships and sampling effects among Lepilemuridae and Lemuridae using a partial cytochrome b gene. *Cytogenetics Research Academy of Science, Paris, Sciences de la vie/Life Sciences* 324:647-656.

Myers, N. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

Nylander, J. A. A. 2004. MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Pastorini, J., M. R. J. Forstner, and R. D. Martin. 2000. Relationships among brown lemurs (*Eulemur fulvus*) based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 16:418-429.

Pastorini, J., R. D. Martin, P. Ehresmann, E. Zimmermann, and M. R. J. Forstner. 2001. Molecular phylogeny of the lemur family Cheirogaleidae (primates) based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 19:45-56.

Pastorini, J., Thalmann, U., and R. D. Martin. 2003. A molecular approach to comparative phylogeography of extant Malagasy lemurs. *Proceedings of the National Academy of Sciences* 100:5879-5884.

Petter, J.-J., and A. Petter-Rousseaux. 1960. Remarques sur la systématique du genre *Lepilemur*. *Mammalia* 24:76-86.

Petter, J.-J., R. Albignac, and Y. Rumpler. 1977. Faune de Madagascar 44: Mammifères Lémuriens (Primates, Prosimiens). ORSTOM/CNRS, Paris, France.

Pope, T. R. 1996. Socioecology, population fragmentation, and patterns of genetic loss in endangered primates. Pp. 119-159 in *Conservation genetics, case histories from nature* (J. C. Avise and J. L. Hamrick, eds.). Chapman and Hall, New York.

Posada, D., and K.A. Crandall. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817-818.

Rasoloarison, R. M., S. M. Goodman, and J. U. Ganzhorn. 2000. Taxonomic revision of mouse lemurs (*Microcebus*) in the western portions of Madagascar. *International Journal of Primatology* 21:963-1019.

Ravaoarimanana, B. 2001. Genetic comparison of wild populations of *Lepilemur septentrionalis* and *Lepilemur dorsalis* using RAPD markers. *Primates* 42:221-231.

Ravaoarimanana, B., R. Tiedemann, D. Montagnon, and Y. Rumpler. 2004. Molecular and cytogenetic evidence for cryptic speciation within a rare endemic Malagasy lemur, the northern sportive lemur (*Lepilemur septentrionalis*). *Molecular Phylogenetics and Evolution* 31:440-448.

Ronquist, F., and J. P. Huelsenbeck. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572-1574.

Rumpler, Y., and R. Albignac. 1975. Intraspecific chromosome variability in a lemur from north of Madagascar: *Lepilemur septentrionalis*, species nova. *American Journal of Physical Anthropology* 42:425-429.

Rumpler, Y., B. Ravaoarimanana, M. Hauwy, and S. Warter. 2001. Cytogenetic arguments in favor of a taxonomic revision of *Lepilemur septentrionalis*. *Folia Primatologica* 72: 308-315.

Sambrook, J., E. F. Fritch, and T. Maniatis. 1989. *Molecular cloning: a laboratory manual*, 2nd edition. Cold Spring Harbor Press, New York.

Saitou, N. and M. Nei. 1987. The neighbour-joining method: a new method for constructing phylogenetic trees. *Molecular Biology and Evolution* 4:406-425.

Schneider, S., D. Roessli, and L. Excofier. 2000. Arlequin: a software for population genetics data analysis. Version 2.000. Genetics and Biometry Laboratory, Department of Anthropology, University of Geneva, Switzerland.

Schwarz, E. 1931. A revision of the genera and species of Madagascar Lemuridae. *Proceedings of the Zoological Society of London* 1931:399-426.

Smith, R. J., and W. L. Jungers. 1997. Body mass in comparative primatology. *Journal of Human Evolution* 32:523-559.

Swofford, D. L. 2001. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b5. Sinauer Associates, Sunderland, Massachusetts.

Tamura, K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzee. *Molecular Biology and Evolution* 10:512-526.

Tattersall, I. 1982. The primates of Madagascar. Columbia University Press, New York.

Telenius, H., N. P. Carter, C. E. Bebb, M. Nordenskjöb, A. J. Ponder, and A. Tunnacliffe. 1992. Degenerate oligonucleotide-primed PCR: general amplification of target DNA by a single degenerate primer. *Genomics* 13:718-725.

Thalmann, U. 2000. Lemur diversity and distribution in western Madagascar - inferences and predictions using a cladistic approach. Pp. 191-202 in *Endémisme et diversité à Madagascar*, Mémoires de la Société de Biogéographie (W. R. Lourenço and S. M. Goodman, eds.). Paris, France.

Thalmann, U., and J. U. Ganzhorn. 2003. *Lepilemur*, sportive lemur. Pp. 1336-1340 in *The natural history of Madagascar* (S. M. Goodman and J. P. Benstead, eds.). The University of Chicago Press, Chicago, Illinois.

Thalmann, U., and T. Geissmann. 2005. New species of woolly lemur *Avahi* (Primates: Lemuriformes) in Bemaraha (Central Western Madagascar). *American Journal of Primatology* 67:371-376.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, and D. G. Higgins. 1997. The ClustalX-Windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 25:4876-4882.

Wheeler, Q. D., and N. I. Platnick. 2000. The phylogenetic species concept (*sensu* Whceeler and Platnick). Pp. 55-69 in *Species concepts and phylogenetic theory: a debate* (Q. D. Wheeler and R. Meier, eds.). Columbia University Press, New York.

Wyner, Y. M., G. Amato, and R. DeSalle. 1999. Captive breeding, reintroduction, and the conservation genetics of black and white ruffed lemurs. *Varecia variegata variegata*. *Molecular Ecology* 8:S107-S115.

Yang, Z., and S. Kumar. 1996. Approximate methods for estimating the pattern of nucleotide substitution rates among sites. *Molecular Biology and Evolution* 13:650-659.

Yoder, A. D., R. M. Rasolofarison, S. M. Goodman, J. A. Irwin, S. Atsalis, M. J. Ravosa, and J. U. Ganzhorn. 2000. Remarkable species diversity of Malagasy mouse lemurs (Primates, *Microcebus*). *Proceedings of the National Academy of Sciences* 97:11325-11330.

Zhang, D.-X., and G. M. Hewitt. 1996. Nuclear integrations: challenges for mitochondrial DNA markers. *Trends in Ecology and Evolution* 11:247-251.

Zimmermann, E., S. Cepok, M. Rakotoarison, V. Zietemann, and U. Radespiel. 1998. Sympatric mouse lemurs in northwest Madagascar; a new rufous mouse lemur species (*Microcebus ravelobensis*). *Folia Primatologica* 69:106-114.

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APPENDIX I

The following Appendices to this publication are available online at the indicated website addresses.

- a. *Lepilemur* Field Data (Individual data file for each *Lepilemur*, including morphometrics, photos, sequence accessions, global position system, microchip data, gender, and location):

<http://10.10.10.3/CCR/Genetics/lemur/index.asp?page=CCR/Genetics/lemur/Megaladapidae.htm>

- b. Map Figure 1 (Maps of historical distributions):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixI.pdf>

- c. Primer Table 1 (Summary of designed primers for D-loop, 12s rRNA, and PAST fragments):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixprimertable1.pdf>

- d. Pairwise Data Table II (Complete pairwise matrices):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixtableII.pdf>

- e. Pairwise Aggregate Analysis Figure 2 (Complete PAA for Summary of the D-loop, 12s rRNA, and PAST fragments):

Figure 2A, D-loop PAA - <http://10.10.10.3/CCR/Genetics/papers/d-loop.pdf>

Figure 2B, 12s rRNA PAA - <http://10.10.10.3/CCR/Genetics/papers/rRNA.pdf>

Figure 2C, PAST PAA - <http://10.10.10.3/CCR/Genetics/papers/pastorini.pdf>

- f. Haplotype Summary List Figure 3 (Summary List of the *Lepilemur* Haplotypes for D-loop, 12s rRNA, and PAST fragments):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixIII.pdf>

- g. Sequence Summary Table III (Summary of the D-loop, 12s rRNA, and PAST fragments):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixtableIII.pdf>

- h. Bayesian D-loop Figure 4 (Bayesian analysis of the D-loop for 211 *Lepilemur*):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixfigure4.pdf>

- i. Message Passing Cluster Figure 5 (Message Passing Cluster analysis of D-loop for 211 *Lepilemur*):

<http://www.omahazoo.com/CCR/Genetics/papers/appendixfigure5.pdf>

APPENDIX II

Samples (211 *Lepilemur* and 19 outgroups total) used in the present genetic study and taxonomic revision of the *Madagascar lemur genus Lepilemur*. ^aTK Number is referenced voucher curated at The Museum of Texas Tech University. ^bMitochondrial DNA sequence data for 12s rRNA (12s rRNA subunit gene), PAST (Pastorini Fragment), and D-loop (D-loop or control region) for each sample are available from GenBank under the listed accession numbers.

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST ^b	D loop ^b
ANAL5	TK125502	Analamera (Antobitasy)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AF474184	AY582564	AY769363
ANAL13	TK125501	Analamera (Antobitasy)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AF474185	AY582565	AY769364
ANAL2.1		Analamera (Analabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192608	AY582566	AY769365
ANAL2.2		Analamera (Analabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192609	AY582567	AY769366
ANAL2.4		Analamera (Analabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192610	AY582568	AY769367
ANAL2.12		Analamera (Analabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192611	AY582569	AY769368
ANAL2.13		Analamera (Analabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192612	AY582570	AY769369
ANAL2.29		Analamera (Ankavavana)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192613	AY582571	AY769370
CAR6		Ankarana (Anilatra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192614	AY582572	AY769371
CAR11		Ankarana (Anilatra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192615	AY582573	AY769372
CAR15		Ankarana (Anilatra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192616	AY582574	AY769373
CAR17		Ankarana (Anilatra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192617	AY582575	AY769374
CAR21		Ankarana (Anilatra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192618	AY582576	AY769375
CAR33		Ankarana (Andriafabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192619	AY582577	AY769376
CAR43		Ankarana (Andriafabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192620	AY582578	AY769377
CAR45		Ankarana (Andriafabé)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	AY192621	AY582579	AY769378

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST ^b	D loop ^b
CAR46		Ankarana (Andriafahabe)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	AY192622	AY582580	AY769379
CAR58		Ankarana (Anilotra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	AY192623	AY582581	AY769380
CAR59		Ankarana (Anilotra)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	AY192624	AY582582	AY769381
MER24	TK125545	Analamera (Antobiarisy)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	AF474211	AY582583	AY769382
MER26		Analamera (Antobiarisy)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	AF474212	AY582584	AY769383
LABE5.1		Analamera (Analabe)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529447	DQ529739	DQ529597
LABE5.2		Analamera (Analabe)	<i>Lepilemур ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529448	DQ529740	DQ529598
LABE5.3		Analamera (Analabe)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529449	DQ529741	DQ529599
LABE5.4		Analamera (Analabe)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529450	DQ529742	DQ529600
LABE5.17		Analamera (Analabe)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529451	DQ529743	DQ529601
FIA5.1		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529422	DQ529714	DQ529572
FIA5.5		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529423	DQ529715	DQ529573
FIA5.6		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529424	DQ529716	DQ529574
FIA5.7		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529425	DQ529717	DQ529575
FIA5.8		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529426	DQ529718	DQ529576
FIA5.9		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529427	DQ529719	DQ529577
FIA5.10		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529428	DQ529720	DQ529578
FIA5.11		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529429	DQ529721	DQ529579
FIA5.12		Andrafiarena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemур ankaranensis</i>	DQ529430	DQ529722	DQ529580

APPENDIX II (CONT.)

LOUIS, JR. ET AL.—ANALYSIS OF THE SPORTIVE LEMURS

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST ^b	D loop ^b
FLA5.13		Andraftamena (Anjakely)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	DQ529431	DQ529723	DQ529581
LAME5.6		Analamera (Ankavanna)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	DQ529420	DQ529712	DQ529570
LAME5.8		Analamera (Ankavanna)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur ankaranensis</i>	DQ529421	DQ529713	DQ529571
FARY5.1	TK125515	Sahafary (Sahafary)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529432	DQ529724	DQ529582
FARY5.2		Sahafary (Sahafary)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529433	DQ529725	DQ529583
FARY5.3		Sahafary (Sahafary)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529434	DQ529726	DQ529584
FARY5.4		Sahafary (Sahafary)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529435	DQ529727	DQ529585
LAVA5.1		Sahafary (Analalava)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529436	DQ529728	DQ529586
LAVA5.2	TK125532	Sahafary (Analalava)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529437	DQ529729	DQ529587
LAVA5.3		Sahafary (Analalava)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529438	DQ529730	DQ529588
LAVA5.4	TK125566	Sahafary (Analalava)	<i>Lepilemur septentrionalis</i>	<i>Lepilemur septentrionalis</i>	DQ529439	DQ529731	DQ529589
KALA24		Kalambatitra (Betanandranano)	<i>Lepilemur microdon</i>	<i>Lepilemur wrightii</i>	DQ529531	DQ529641	DQ529499
KALA4.9	TK125527	Kalambatitra (Befarara)	<i>Lepilemur microdon</i>	<i>Lepilemur wrightii</i>	DQ529356	DQ529646	DQ529504
KALA4.16	TK125565	Kalambatitra (Befarara)	<i>Lepilemur microdon</i>	<i>Lepilemur wrightii</i>	DQ529357	DQ529647	DQ529505
KALA4.18	TK125526	Kalambatitra (Befarara)	<i>Lepilemur microdon</i>	<i>Lepilemur wrightii</i>	DQ529358	DQ529648	DQ529506
KALA4.19		Kalambatitra (Befarara)	<i>Lepilemur microdon</i>	<i>Lepilemur wrightii</i>	DQ529359	DQ529649	DQ529507
KALA5.12		Darana (Sahalava)	<i>Lepilemur microdon</i>	<i>Lepilemur wrightii</i>	DQ529419	DQ529711	DQ529569
DARA4.7	TK125516	Darana (Andranotsimay)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoii</i>	DQ529329	DQ529619	DQ529477
DARA4.17	TK125517	Darana (Andranotsimay)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoii</i>	DQ529330	DQ529620	DQ529478

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12S rRNA ^b	PAST ^b	D loop ^b
DAR4.18	TK125564	Daraina	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529331	DQ529621	DQ529479
DAR4.19		Daraina	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529332	DQ529622	DQ529480
DAR4.23		Daraina	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529333	DQ529623	DQ529481
DAR4.27		Daraina	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529334	DQ529624	DQ529482
DAR4.28		Daraina (Andranotsimaty)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529335	DQ529625	DQ529483
DAR4.30		Daraina (Andranotsimaty)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529336	DQ529626	DQ529484
DAR4.35		Daraina (Andranotsimaty)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529337	DQ529627	DQ529485
DAR4.41		Daraina (Andranotsimaty)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)	DQ529338	DQ529628	DQ529486
DAR5.1		Daraina (Andranotsimaty)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)			
DAR5.2		Daraina (Andranotsimaty)	<i>Lepilemur ankaranensis</i>	<i>Lepilemur milanoi</i> (Andranotsimaty)			
GARI	TK125518	Manongarivo	<i>Lepilemur dorsalis</i>	<i>Lepilemur dorsalis</i>	AY192625	AY582592	AY769391
ANT5.2		Antafondro (Maromiaandra)	<i>Lepilemur dorsalis</i>	<i>Lepilemur dorsalis</i>	DQ529440	DQ529732	DQ529590
ANT5.5		Antafondro (Maromiaandra)	<i>Lepilemur dorsalis</i>	<i>Lepilemur dorsalis</i>	DQ529441	DQ529733	DQ529591
ANT5.6		Antafondro (Maromiaandra)	<i>Lepilemur dorsalis</i>	<i>Lepilemur dorsalis</i>	DQ529442	DQ529734	DQ529592
ANT5.7	TK125507	Antafondro (Maromiaandra)	<i>Lepilemur dorsalis</i>	<i>Lepilemur dorsalis</i>	DQ529443	DQ529735	DQ529593
ANT5.11	TK125562	Antafondro (Maromiaandra)	<i>Lepilemur dorsalis</i>	<i>Lepilemur dorsalis</i>	DQ529444	DQ529736	DQ529594
LAZA5.1	TK125533	Sahamalaza (Ankarafana)	<i>Lepilemur dorsalis</i>	<i>Lepilemur sahamalazensis</i>	DQ529445	DQ529737	DQ529595
LAZA5.10	TK125534	Sahamalaza (Ankarafana)	<i>Lepilemur dorsalis</i>	<i>Lepilemur sahamalazensis</i>	DQ529446	DQ529738	DQ529596
LOKO4.2	TK125535	Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tymerlachsoni</i>	DQ529360	DQ529650	DQ529508

APPENDIX II (CONT.)

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Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s rRNA ^c	PAST ^b	D loop ^b
LOKO4.5	TK125537	Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529361	DQ529651	DQ529509
LOKO4.19		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529362	DQ529652	DQ529510
LOKO4.20		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529363	DQ529653	DQ529511
LOKO4.23		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529364	DQ529654	DQ529512
LOKO4.32		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529365	DQ529655	DQ529513
LOKO4.33	TK125536	Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529366	DQ529656	DQ529514
LOKO4.34		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529367	DQ529657	DQ529515
LOKO4.35		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529368	DQ529658	DQ529516
LOKO4.36		Lokobe	<i>Lepilemur dorsalis</i>	<i>Lepilemur tamerlachsoni</i>	DQ529369	DQ529659	DQ529517
ANK4		Ankarafantsika	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	AF474186	AY582585	AY769384
ANK16		Ankarafantsika	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	AF474187	AY582586	AY769385
KIBO22	TK125529	Tsiombikibo	<i>Lepilemur aecclis</i>	<i>Lepilemur ahmansi</i>	DQ529312	DQ529602	DQ529460
KIBO58	TK125530	Tsiombikibo	<i>Lepilemur edwardsi</i>	<i>Lepilemur ahmansi</i>	DQ529313	DQ529603	DQ529461
KIBO65	TK125531	Tsiombikibo	<i>Lepilemur edwardsi</i>	<i>Lepilemur ahmansi</i>	DQ529314	DQ529604	DQ529462
KIBO68		Tsiombikibo	<i>Lepilemur aecclis</i>	<i>Lepilemur ahmansi</i>	DQ529315	DQ529605	DQ529463
MARI		Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529316	DQ529606	DQ529464
MAR2		Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529317	DQ529607	DQ529465
MAR18	TK125541	Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529318	DQ529608	DQ529466
MAR20	TK125542	Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529319	DQ529609	DQ529467

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12S rRNA ^b	PAST ^b	D loop
MAR21		Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529320	DQ529610	DQ529468
MAR22	TK125543	Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529321	DQ529611	DQ529469
MAR23		Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529322	DQ529612	DQ529470
MAR27		Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529323	DQ529613	DQ529471
MAR36	TK125544	Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529324	DQ529614	DQ529472
MAR38		Mariarano	<i>Lepilemur edwardsi</i>	<i>Lepilemur edwardsi</i>	DQ529325	DQ529615	DQ529473
HH21	TK125519	Anjiamangirana	<i>Lepilemur edwardsi</i>	<i>Lepilemur grewcocki</i>	DQ529326	DQ529616	DQ529474
HH22	TK125520	Anjiamangirana	<i>Lepilemur edwardsi</i>	<i>Lepilemur grewcocki</i>	DQ529327	DQ529617	DQ529475
HH23	TK125521	Anjiamangirana	<i>Lepilemur edwardsi</i>	<i>Lepilemur grewcocki</i>	DQ529328	DQ529618	DQ529476
AND65		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529329	DQ529629	DQ529487
AND66	TK125503	Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529340	DQ529630	DQ529488
AND67	TK125560	Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529341	DQ529631	DQ529489
AND68	TK125561	Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529342	DQ529632	DQ529490
AND69		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529343	DQ529633	DQ529491
AND78		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529344	DQ529634	DQ529492
AND79		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529345	DQ529635	DQ529493
AND92		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529346	DQ529636	DQ529494
AND93		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529347	DQ529637	DQ529495
AND94		Andohahela (Mangatsiaka)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529348	DQ529638	DQ529496

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12S rRNA ^b	PAST ^c	D loop ^c
AZO5.6		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529409	DQ529701	DQ529559
HAZO5.7		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529410	DQ529702	DQ529560
HAZO5.16		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529411	DQ529703	DQ529561
HAZO5.17		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529412	DQ529704	DQ529562
HAZO5.18		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529413	DQ529705	DQ529563
HAZO5.19		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529414	DQ529706	DQ529564
HAZO5.20		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529415	DQ529707	DQ529565
HAZO5.21		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529416	DQ529708	DQ529566
HAZO5.22		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529417	DQ529709	DQ529567
HAZO5.23		Andohahela (Ihazofotsy)	<i>Lepilemur leucopus</i>	<i>Lepilemur leucopus</i>	DQ529418	DQ529710	DQ529568
BEZ14		Béza-Mahafaly	<i>Lepilemur leucopus</i>	<i>Lepilemur petteri</i>	AF474191	AY582587	AY769386
BEZ15	TK125511	Béza-Mahafaly	<i>Lepilemur leucopus</i>	<i>Lepilemur petteri</i>	AF474192	AY582588	AY769387
BEZ18	TK125563	Béza-Mahafaly	<i>Lepilemur leucopus</i>	<i>Lepilemur petteri</i>	AF474193	AY582589	AY769388
BEZ21	TK125512	Béza-Mahafaly	<i>Lepilemur leucopus</i>	<i>Lepilemur petteri</i>	AF474194	AY582590	AY769389
BEZ22		Béza-Mahafaly	<i>Lepilemur leucopus</i>	<i>Lepilemur petteri</i>	AF474195	AY582591	AY769390
KEL1	TK125528	Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	DQ529390	DQ529682	DQ529540
RANO234	TK125552	Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AF474218	AY582596	AY769395
RANO235		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AF474219	AY582597	AY769396
RANO236		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AF474220	AY582598	AY769397

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12S rRNA ^b	PAST ^b	D loop ^b
RANO2.24		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AY585736	DQ529678	DQ529536
RANO2.25		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AY585737	DQ529679	DQ529537
RIR02		Ranomafana (Maharitra)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	DQ529407	DQ529699	DQ529557
RAN3.1		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	DQ529408	DQ529700	DQ529558
PBZT111		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AY254494	AY582600	AY769399
TOL2.17	TK125555	Tolongoma	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	AF474224	AY582599	AY769398
VOP2.6		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	DQ529388	DQ529680	DQ529538
VOP2.16		Ranomafana (Vohiparara)	<i>Lepilemur microdon</i>	<i>Lepilemur microdon</i>	DQ529389	DQ529681	DQ529539
MIT16		Anjahamena (Vohiparara)	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	AF474213	AY582604	AY769403
MIT17	TK125546	Anjahamena	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur aecclis</i>	AF474214	AY582605	AY769404
PBZT112	TK125551	Anjahamena	<i>Lepilemur edwardsi</i>	<i>Lepilemur aecclis</i>	AY254493	AY582606	AY769405
PBZT119		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529380	DQ529670	DQ529528
JAM4.8		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529381	DQ529671	DQ529529
JAM4.9		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529382	DQ529672	DQ529530
JAM4.10	TK125522	Anjahamena	<i>Lepilemur edwardsi</i>	<i>Lepilemur aecclis</i>	DQ529383	DQ529673	DQ529531
JAM4.11		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529384	DQ529674	DQ529532
JAM4.12		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529385	DQ529675	DQ529533
JAM4.13		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529386	DQ529676	DQ529534
JAM4.27		Anjahamena	<i>Lepilemur aecclis</i>	<i>Lepilemur aecclis</i>	DQ529387	DQ529677	DQ529535

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12S rRNA ^b	PAST ^c	D loop ^b
AND20	TK125559	Andohahela (Manangotry)	<i>Lepilemur microdon</i>	<i>Lepilemur fimbriata</i>	DQ529401	DQ529693	DQ529551
ANJZ32	TK125504	Anjozorobe (Amboasary)	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529349	DQ529639	DQ529497
ANJZ33	TK125505	Anjozorobe (Amboasary)	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529350	DQ529640	DQ529498
ANOSIB15		Anosibe an'ala	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474188	AY582607	AY769406
ANOSIB18	TK125506	Anosibe an'ala	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474189	AY582608	AY769407
BET21		Betampona	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474190	AY582609	AY769408
FAN10		Fandriana	<i>Lepilemur mustelinus</i>	<i>Lepilemur betsileo</i>	AF474196	AY582610	AY769409
FAN11	TK125513	Fandriana	<i>Lepilemur microdon</i>	<i>Lepilemur betsileo</i>	AF474197	AY582611	AY769410
FAN424	TK125514	Fandriana	<i>Lepilemur microdon</i>	<i>Lepilemur betsileo</i>	DQ529400	DQ529692	DQ529550
JOZO4.11		Anjozorobe (Amboasarinala)	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529355	DQ529645	DQ529503
L5		Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474201	AY582620	AY769420
M83B		Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474202	AY582612	AY769411
M93B		Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474203	AY582613	AY769412
M94B		Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474204	AY582614	AY769413
M95B		Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474205	AY582615	AY769414
M104B		Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474206	AY582616	AY769415
M105B	TK125538	Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474207	AY584480	AY769416
M140	TK125539	Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474208	AY582617	AY769417
M141	TK125539	Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur jamesi</i>	AF474209	AY582618	AY769418

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST ^c	D loop ^b
M142	TK125540	Manombo	<i>Lepilemur microdon</i>	<i>Lepilemur janesi</i>	AF474210	AY582619	AY769419
MIZA3	TK125547	Maromizaha	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529403	DQ529695	DQ529553
MIZA11		Maromizaha	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529404	DQ529696	DQ529554
MIZA15		Maromizaha	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529405	DQ529697	DQ529555
MIZA18		Maromizaha	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529406	DQ529698	DQ529556
SIN26		Tsinjoarivo	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474221	AY582621	AY769421
SIN27		Tsinjoarivo	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474222	AY582622	AY769422
TAD25		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474223	AY582623	AY769423
TAD4.4	TK125554	Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529391	DQ529683	DQ529541
TAD4.16	TK125553	Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529392	DQ529684	DQ529542
TAD4.17		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529393	DQ529685	DQ529543
TAD4.19		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529394	DQ529686	DQ529544
TAD4.23		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529395	DQ529687	DQ529545
TAD4.58		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529396	DQ529688	DQ529546
TAD4.59		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529397	DQ529689	DQ529547
TAD4.60		Tsinjoarivo	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529398	DQ529690	DQ529548
TAD4.61		Mantadia	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	DQ529399	DQ529691	DQ529549
TSINJ36		Tsinjoarivo	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474225	AY582624	AY769424
TSINJ37		Tsinjoarivo	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474226	AY582625	AY769425
ZAH21		Zahamena	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474227	AY582626	AY769426

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12 _s rRNA ^b	PAST ^b	D loop ^b
ZAH22		Zahamena	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474228	AY582627	AY769427
ZAH25		Zahamena	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474229	AY582628	AY769428
ZAH201		Zahamena	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474230	AY582629	AY769429
ZAH216		Zahamena	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474231	AY582630	AY769430
ZAH217		Zahamena	<i>Lepilemur mustelinus</i>	<i>Lepilemur mustelinus</i>	AF474232	AY582631	AY769431
MOR117	TK125548	Beroboka	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur ruficaudatus</i>	AF474215	AY582601	AY769400
MOR142	TK125549	Beroboka	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur ruficaudatus</i>	AF474216	AY582602	AY769401
MOR147	TK125550	Beroboka	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur ruficaudatus</i>	AF474217	AY582603	AY769402
BEMA5	TK125508	Tsingy de Bemaraha	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur randrianasoli</i>	DQ529370	DQ529660	DQ529518
BEMA6	TK125509	Tsingy de Bemaraha	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur randrianasoli</i>	DQ529371	DQ529661	DQ529519
BEMA7	TK125510	Tsingy de Bemaraha	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur randrianasoli</i>	DQ529372	DQ529662	DQ529520
ZOMB8		Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529373	DQ529663	DQ529521
ZOMB9	TK125558	Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529374	DQ529664	DQ529522
ZOMB12	TK125556	Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529375	DQ529665	DQ529523
ZOMB15	TK125557	Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529376	DQ529666	DQ529524
ZOMB16		Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529377	DQ529667	DQ529525
ZOMB21		Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529378	DQ529668	DQ529526
ZOMB52		Zombitse	<i>Lepilemur ruficaudatus</i>	<i>Lepilemur hubbardi</i>	DQ529379	DQ529669	DQ529527
JAR2	TK125523	Anhanaharibe-Sud	<i>Lepilemur mustelinus</i>	<i>Lepilemur scali</i>	AF474198	AY582593	AY769392

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s	PAST ^b rRNA ^b	D loop ^b
JAR3	TK125524	Anhanaharibe-Sud	<i>Lepilemur mustelinus</i>	<i>Lepilemur seali</i>	AF474199	AY582594	AY769393
JAR8	TK125525	Anhanaharibe-Sud	<i>Lepilemur mustelinus</i>	<i>Lepilemur seali</i>	AF474200	AY582595	AY769394
JAR3.38		Anhanaharibe-Sud	<i>Lepilemur mustelinus</i>	<i>Lepilemur seali</i>	DQ529352	DQ529642	DQ529500
JAR3.39		Anhanaharibe-Sud	<i>Lepilemur mustelinus</i>	<i>Lepilemur seali</i>	DQ529353	DQ529643	DQ529501
JAR3.46		Anhanaharibe-Sud	<i>Lepilemur mustelinus</i>	<i>Lepilemur seali</i>	DQ529354	DQ529644	DQ529502
NARA4.20		Mananara-Nord (Ivontaka-Sud)	<i>Lepilemur mustelinus</i>	<i>Lepilemur seali</i>	DQ529402	DQ529694	DQ529552
RANO261		Ranomafana	<i>Avahi laniger</i>	<i>Avahi laniger</i>	AF474233	AY582559	AY584496
RANO67		Ranomafana	<i>Avahi laniger</i>	<i>Avahi laniger</i>	AY254047	AY582558	AY584495
ANK33		Ankarafantsika	<i>Avahi occidentalis</i>	<i>Avahi occidentalis</i>	AF474241	AY582560	AY584497
RANO332		Ranomafana	<i>Propithecus edwardsi</i>	<i>Propithecus edwardsi</i>	AF474236	AY582556	AY585739
MOR68		Beroboka	<i>Propithecus verreauxi</i>	<i>Propithecus verreauxi</i>	AF474237	AY582557	AF585739
RANO45		Ranomafana	<i>Eulemur fulvus rufus</i>	<i>Eulemur fulvus rufus</i>	AF474234	AY582561	AY585738
FAN21		Fandriana	<i>Varécia variegata variegata</i>	<i>Varécia variegata variegata</i>	AF474235	AY582555	AY584494
RANO250		Ranomafana	<i>Microcebus rufus</i>	<i>Microcebus rufus</i>	AY582713	AY582546	AY159722
ANK7		Ankarafantsika	<i>Microcebus ravelobensis</i>	<i>Microcebus ravelobensis</i>	AY582712	AY582545	AY159695
KIAN124		Kianjavato	<i>Hapalemur simus</i>	<i>Hapalemur simus</i>	AF474238	AY582548	AY584488
RANO338		Ranomafana	<i>Hapalemur simus</i>	<i>Hapalemur simus</i>	AY582714	AY582547	AY254049
RANO351		Ranomafana	<i>Hapalemur aureus</i>	<i>Hapalemur aureus</i>	AF474239	AY582549	AY584489
RANO352		Ranomafana	<i>Hapalemur aureus</i>	<i>Hapalemur aureus</i>	AY582715	AY582550	AY254048

APPENDIX II (CONT.)

Catalog Number	TK Number ^a	Location	Original Species Designation	Current Species Designation	12s rRNA ^b	PAST ^b	D loop ^b
RANO61		Ranomafana	<i>Hapalemur griseus griseus</i>	<i>Hapalemur griseus griseus</i>	AY582716	AY582551	AY584490
RANO62		Ranomafana	<i>Hapalemur griseus griseus</i>	<i>Hapalemur griseus griseus</i>	AY582717	AY582552	AY584491
ANAL2.23		Analamerina	<i>Hapalemur griseus occidentalis</i>	<i>Hapalemur griseus occidentalis</i>	AY582718	AY582554	AY584493
GAR9		Manongarivo	<i>Hapalemur griseus occidentalis</i>	<i>Hapalemur griseus occidentalis</i>	AY582719	AY582553	AY584492
RANO229		Ranomafana	<i>Cheirogaleus major</i>	<i>Cheirogaleus major</i>	AF474240	AY582563	AY254050
GAR8		Manongarivo	<i>Cheirogaleus medius</i>	<i>Cheirogaleus medius</i>	AY192626	AY582562	AY584498

